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VOLUME 31 MARCH, 1953 NUMBER 2

NUTRITIONAL REQUIREMENTS OF *ARTHROBACTER TERREGENS*[1]

BY MARGARET O. BURTON[2] AND A. G. LOCHHEAD[3]

Abstract

Vitamin and amino acid requirements have been established for *Arthrobacter terregens* n. sp., an organism found to require an unknown growth factor present in soil extract, liver extract, and culture filtrates of *Arthobacter pascens* n. sp. Apart from this unknown factor, concentrates of which promote growth at less than 0.1 μgm. per ml., biotin, thiamine, and pantothenic acid were found to be essential. With adequate mineral supplement the nitrogen requirements could be fulfilled by *l*-glutamic acid, though the latter could be replaced by combinations of other amino acids.

Introduction

Recent studies in this laboratory (1, 2) have resulted in the isolation of a soil organism whose nutritional requirements include a factor present in soil extract, liver extract, and culture filtrates of certain soil bacteria. The organism, *Arthrobacter terregens*, previously described and named (1), has been employed as the test organism for the detection and measurement of the factor in natural products and culture filtrates. In the development of an assay procedure, the nutrition of the test organism has been studied with the object of establishing, in so far as possible, a chemically defined medium. The present report deals with the vitamin and amino acid requirements of *A. terregens*.

Experimental

Following the isolation of *A. terregens* from soil on soil extract agar, the organism was cultured for optimum growth on a medium of inorganic salts, glucose, yeast extract, and soil extract. The soil extract, which contained an essential factor, was shortly replaced by low concentrations of culture filtrate obtained when the soil organism *Arthrobacter pascens* (No. *B*89) was grown in a simple liquid medium containing minerals, inorganic nitrogen, and glucose (1), 0.1 ml. of centrifuged culture fluid per 100 ml. of an otherwise nutritionally adequate medium providing optimum growth of *A. terregens*. A complete medium for the organism was prepared by adding the following to

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[The January number of this Journal (Can. J. Botany, 31 : 1–144. 1953) was issued January 27, 1953.]

1 liter of distilled water: monohydrogen potassium phosphate, 1.0 gm.; potassium nitrate, 0.5 gm.; $MgSO_4 .7H_2O$, 0.2 gm.; calcium chloride, 0.1 gm.; sodium chloride, 0.1 gm.; $FeCl_3 . 6H_2O$, 0.01 gm. The solution was adjusted to pH 6.8, heated to boiling, allowed to cool, and filtered, after which 1.0 gm. yeast extract, 1.0 gm. glucose, and 1.0 ml. culture filtrate of *A. pascens* were added. Throughout this paper the salt mixture is referred to as "basal salts", and the procedure of heating and filtering is as outlined above.

For the detection and measurement of growth the complete medium minus test ingredients was prepared in 5/4 of the final concentration and a series of 40-ml. quantities measured out, depending upon the number of portions to be tested. After addition of the test materials, the volumes were made up to 50 ml. in all cases and 10-ml. portions added to quadruplicate 50-ml. Erlenmeyer flasks. After sterilization, the contents of the flasks were inoculated with one drop of a suspension of *A. terregens* prepared by centrifuging 10.0 ml. of a four- to five-day culture in the complete medium, washing three times in sterile saline, and finally making up to 10 ml. After 70 hr. incubation at 20° C., turbidity measurements were made by a Unicam spectrophotometer at a wave length of 450 mμ allowing for uninoculated controls. Results are expressed as the average optical density of quadruplicate cultures.

Vitamin Requirements

It has been shown (1) that optimum growth of *A. terregens* is obtained in a medium containing, in addition to basal salts and glucose, both yeast extract and culture filtrate of *A. pascens* (*B*89). As indicated in Table I, neither of these ingredients alone is able to promote growth of the test organism. Table I further shows that neither casein hydrolyzate (Difco "casamino acids") nor a combination of 13 vitamins was able to replace yeast extract; however, casein hydrolyzate when supplemented by the vitamins provided a satisfactory replacement. The vitamins were added in the following amounts per 100 ml.

TABLE I

REPLACEMENT OF YEAST EXTRACT BY CASAMINO ACIDS AND VITAMINS FOR GROWTH OF *Arthrobacter terregens*

Addenda to basal salts + glucose	Optical density (aver. 4 tests)
None	.005
Yeast extract (0.1%)	.008
Culture filtrate *B*89 (0.1 ml./100 ml.)	.008
Yeast extract + culture filtrate *B*89	.199
Casamino acids (0.1%) + culture filtrate *B*89	.006
13 vitamins (see text) + culture filtrate *B*89	.008
Casamino acids + 13 vitamins	.006
Casamino acids + vitamins + culture filtrate *B*89	.152

medium: thiamine, 40 μgm.; pyridoxal, 40 μgm.; pyridoxamine, 4 μgm.; pyridoxine, 40 μgm.; calcium pantothenate, 40 μgm.; nicotinic acid, 40 μgm.; riboflavin, 40 μgm.; *p*-aminobenzoic acid, 40 μgm.; folic acid, 4 μgm.; choline, 80 μgm.; inositol, 2 mgm.; biotin, 0.1 μgm.; and vitamin B_{12}, 0.4 μgm.

The results indicate that the growth-promoting effect of yeast extract is to be ascribed partly to its amino acid content and partly to the presence of vitamins. The specific vitamin requirements were determined by experiments in which the vitamins were omitted, singly or in groups, from a medium of basal salts, glucose, casamino acids, and culture filtrate *B*89. As demonstrated in Table II, only thiamine, calcium pantothenate, and biotin were essential for growth of *A. terregens;* for all three of these a clear-cut need was evident. It was found that growth in the presence of the three vitamins was not increased by the addition of yeast extract, but was somewhat greater when the concentrations of the essential vitamins were doubled.

TABLE II

VITAMIN REQUIREMENTS OF *Arthrobacter terregens*

Addenda to medium*	Optical density (aver. 4 tests)
None	.001
13 B vitamins	.132
13 B vitamins minus thiamine	.015
" minus pyridoxine, pyridoxal, pyridoxamine	.132
" minus calcium pantothenate	.005
" minus nicotinic acid	.126
" minus riboflavin	.127
" minus *p*-aminobenzoic acid	.130
" minus folic acid	.129
" minus choline	.124
" minus inositol	.108
" minus biotin	.005
" minus vitamin B_{12}	.120

* *Basal salts, glucose, casamino acids, culture filtrate B89.*

Amino Acid Requirements

From the results recorded in Table III, it is observed that casamino acids were able to supply the nitrogen requirements of *A. terregens*, though inorganic nitrogen as either potassium nitrate or ammonium chloride was inadequate. Although a combination of 24 amino acids (listed below) gave partial response of the test organism, growth approximating that obtained with casamino acids could not be attained unless an inorganic source of nitrogen such as ammonium chloride or sodium ammonium hydrogen phosphate was also present. The effect of casamino acids in an otherwise complete medium could therefore be duplicated by employing 24 amino acids in addition to 0.1% sodium ammonium hydrogen phosphate (Table III).

TABLE III

NITROGEN REQUIREMENTS OF *Arthrobacter terregens*

Nitrogen sources added to medium*	Optical density (aver. 4 tests)
Casamino acids (0.1%)	.262
Casamino acids + KNO_3	.226
KNO_3	.011
NH_4Cl (0.05%)	.009
Casamino acids (0.1%)	.206
24 amino acids (see text)	.067
24 amino acids + casamino acids	.189
" + KNO_3 (0.05%)	.060
" + NH_4Cl (0.05%)	.171
" + NH_4Cl (0.1%)	.171
" + NH_4Cl (0.2%)	.143
" + $NaNH_4HPO_4$ (0.1%)	.180
" + urea (0.1%)	.094

* *Basal salts (minus KNO_3), glucose, culture filtrate B89, thiamine (80 μgm./100 ml.), calcium pantothenate (80 μgm. /100 ml.), biotin (0.2 μgm./100 ml.).*

In order to determine the amino acids essential to the growth of *A. terregens*, media were prepared in which each of the following groups of amino acids, respectively, was omitted from the complete medium:—

Group I—glycine, 0.0005%; *dl*-alanine, 0.0055%; *dl*-serine, 0.0077%; *dl*-norleucine, 0.002%; *dl*-threonine, 0.0038%;

Group II—*dl*-leucine, 0.0097%; *dl*-valine, 0.0065% *dl*-isoleucine, 0.0063%;

Group III—*dl*-aspartic acid, 0.0061%; *l*-glutamic acid, 0.0233%;

Group IV—*l*-arginine, 0.0043%; *l*-lysine, 0.0075%; *l*-asparagine, 0.0020%; *dl*-ornithine, 0.0020%;

Group V—*l*-histidine, 0.0021%; *l*-proline, 0.0078%; *l*-hydroxyproline, 0.00023%;

Group VI—*dl*-phenylalanine, 0.0058%; *dl*-tryptophane, 0.0012%; *l*-tyrosine, 0.0067%.

Group VII—*dl*-methionine, 0.0034%; *l*-cysteine, 0.0002%; *l*-cystine, 0.0002%; *l*-taurine, 0.0003%.

The results recorded in Table IV indicate that no single group was essential to the nutrition of the organism, and that in the absence of each group, substitution effects were evident with good to optimum growth resulting. Various combinations that were able to provide optimum growth included groups III and IV, and Groups V, VI, and VII. When these five groups were tested individually in an otherwise complete medium, only group III was found to provide the necessary amino acids for growth; when the individual

TABLE IV

AMINO ACID REQUIREMENTS OF *Arthrobacter terregens*

Addenda to medium*	Optical density (aver. 4 tests)
None	.005
Casamino acids (0.1%)	.167
7 amino acid groups (see text)	.134
7 amino acid groups minus Group I	.147
" " minus Group II	.151
" " minus Group III	.168
" " minus Group IV	.148
" " minus Group V	.146
" " minus Group VI	.139
" " minus Group VII	.099
Amino acids, Groups I, II	.033
Amino acids, Groups III, IV	.180
Amino acids, Groups V, VI, VII	.171
None	.006
Casamino acids (0.1%)	.173
Amino acids, Group III	.141
Amino acids, Group IV	.006
Amino acids, Group V	.006
Amino acids, Group VI	.012
Amino acids, Group VII	.008
Casamino acids (0.1%)	.122
Amino acids, Group III	.109
Aspartic acid of Group III (.0061%)	.003
l-Glutamic acid of Group III (.0233%)	.074
Casamino acids (0.1%)	.201
l-Glutamic acid (.0233%)	.211
" " + Group I	.144
" " + Group II	.121
" " + Group III	.185
" " + Group IV	.189
" " + Group V	.192
" " + Group VI	.172
" " + Group VII	.170

* *Basal salts (minus KNO_3), glucose, three vitamins, culture filtrate B89, $NaNH_4HPO_4$.*

amino acids of the group were tested, *l*-glutamic acid proved to be the essential compound. Employing *l*-glutamic acid (0.023%) as sole source of amino nitrogen in the complete medium containing, per 100 ml., basal salts (minus potassium nitrate); glucose, 0.1 gm.; sodium ammonium hydrogen phosphate, 0.1 gm.; thiamine, 80 μgm.; calcium pantothenate, 80 μgm.; biotin, 0.2 μgm., and culture filtrate *B*89, 0.1 ml., growth of *A. terregens* could not be further stimulated by the additions of each of the seven groups of amino acids. *l*-Glutamic acid was thus found to fulfil the amino nitrogen requirements of the organism although combinations of other amino acids could substitute for glutamic acid.

Discussion

A medium containing inorganic salts, glucose, three vitamins, and one amino acid cannot be regarded as entirely chemically defined after the addition of the unknown essential factor required for growth of *A. terregens*, either in the form of a small portion of culture fluid (1 part per 1000) or even of small additions of concentrates of the active factor which have been found to give good response at concentrations of less than 0.1 μgm. per ml. Conceivably such addenda may be sources of very small quantities of amino acids or vitamins in addition to the unknown factor. A previous paper (1) showed that the iron porphyrin compound, hemin, was capable of replacing in part the stimulation shown by the culture filtrate. When hemin was substituted for the culture filtrate, growth in a defined medium containing vitamins and glutamic acid was equal to that obtained in a hemin–yeast extract medium. This suggests that the three vitamins and one amino acid of the defined medium are the essential nutrients supplied by the yeast extract, while the culture filtrate provides only the essential factor or factors, not present in yeast extract though partly replaceable by hemin, required by *A. terregens*.

As vitamin B_{12} may be present in small amounts in the culture filtrate but not in yeast extract, the deficiency of this vitamin in a medium of yeast extract and hemin might result in the limited response by the organism to hemin compared to the culture filtrate. However, the addition of vitamin B_{12} to the yeast extract – hemin medium did not influence the growth of *A. terregens*, and this vitamin is therefore considered to be nonessential in the nutrition of the organism.

Further tests were made to examine the possibility that mutant cells of *A. terregens*, comprising a small fraction of the inoculum used in these experiments, might become adjusted to the more definitive media and show maximum turbidity at the end of the 70-hr. incubation period. In higher dilutions of the inoculum such mutants might be expected to be eliminated, the better defined medium, unlike that containing yeast extract, then being unable to support growth of the lighter inoculum. Serial dilutions of the inoculum were prepared from 10^{-1} to 10^{-7}, one loopful of each being added respectively to tubes of three semisolid agar media, all containing basal salts, glucose, and culture filtrate *B*89, but with different addenda as follows:

(i) — yeast extract

(ii) — three vitamins and casamino acids

(iii) — three vitamins, *l*-glutamic acid, and $NaNH_4HPO_4$.

Though no growth occurred in the tubes inoculated with one loopful of the 10^{-7} dilution, equal growth resulted in all three media with dilutions up to 10^{-6}, suggesting that the development of *A. terregens* in the more defined media was not attributable to adaptive mutants.

Acknowledgment

The authors wish to acknowledge the very effective assistance rendered by Miss Winnifred Ryan during the investigation.

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FERTILITY AND POLYPLOIDY OF *EUPHORBIA CYPARISSIAS* IN CANADA[1]

By R. J. Moore and D. R. Lindsay[2]

Abstract

Euphorbia cyparissias L., a European species originally introduced into North America as an ornamental, is now firmly established on roadsides and pastures in Eastern Canada. The Canadian distribution is mapped from specimens in three herbaria. Plants with a somatic chromosome number of 20 and plants with the number $2n = 40$ occur in eastern Ontario and adjacent Quebec. According to all available evidence for this region, the diploid plants never set seed, whereas the tetraploid populations are highly fertile. The cells of the upper leaf epidermis of the tetraploid plants are conspicuously larger than those of the diploid plants. By means of this criterion, the probable chromosome number of herbarium specimens was determined. The distribution of the diploid and tetraploid plants in Ontario and western Quebec is mapped. Tetraploid plants are known from eight locations in this area; five of these infestations are serious. It is believed that the sterility of the diploid populations is due to a genic condition which may interrupt normal pollen development.

Introduction

Cypress spurge (*Euphorbia cyparissias* L.) is a European perennial herb that was introduced into North America as an ornamental plant. Frequently the species has been planted in graveyards, from which it escaped to become widely distributed in the older settled areas of Eastern Canada. Large areas of pastureland in some districts are so heavily polluted with this weed that grazing is no longer practicable. Further, cypress spurge contains a toxic milky juice that has caused a severe dermatitis in sensitive individuals in one infested area in Ontario. Cattle poisoning has also been reported from the United States (14).

It was noted, during weed surveys carried out in Ontario in the past few years, that most stands of the weed set no seed. However, several large infestations bore abundant seed. The more common lack of seed production in North America has been mentioned by previous workers.

In an attempt to discover the cause of the apparent sterility of many clones, a cytogenetic study was undertaken. It was discovered that both diploid ($2n = 20$) and tetraploid plants occur in Ontario and western Quebec and that a relationship seems to exist between chromosome number and fertility. In all cases, the sterile plants proved to be diploid; the fertile plants, tetraploid. It was observed also that the size of the epidermal cells of the leaves was correlated with the chromosome number. This provided a convenient method of classing herbarium specimens as probable diploid or tetraploid plants.

[1] *Manuscript received July 9, 1952.*

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[2] *Associate Botanist (Cytogenetics) and Assistant Botanist (Weed Investigations), respectively.*

Materials and Methods

The chromosome counts were made from root-tip preparations of plants collected in the Ottawa district and eastern Ontario. Field observations of the extent and fertility of the infestations were made and a representative clump of the plants was dug up and brought back for further study. Herbarium specimens of the collections are preserved in the Herbarium of the Division of Botany and Plant Pathology, Science Service, Department of Agriculture, Ottawa. Herbarium specimens examined in the preparation of Fig. 1 are from the above herbarium and, as well, from that of the National Museum of Canada, Ottawa, and the Montreal Botanical Garden.

Root tips were left in water in a refrigerator at 2-4° C. for two hours, fixed in Randolph's Nawaschin solution, embedded in paraffin, and sectioned in the usual manner. The preparations were stained in crystal violet stain.

Measurements of the area of the epidermal cells of the leaf were made from cellulose acetate peels. To prepare the peels, cellulose acetate was dissolved in acetone; approximately one volume of acetate to two volumes of acetone. A drop of the mixture was spread evenly on the leaf surface. After two to five minutes the dried peel was easily stripped from the leaf and mounted on a microscope slide, under a cover glass. Often it is desirable to place a weight on the cover glass for an hour or two to flatten the peel. The impression of the cell walls is easily seen on the dry peel. In the case of herbarium specimens, the leaf was removed and boiled in water for one to two minutes, spread on a glass slide, and blotted dry. The peel was then made in the usual manner.

Measurement of the cell areas was made by a modification of the method of Ashby (1). A squared area of an ocular micrometer outlined an area of 16,950 sq. μ at a magnification of $\times 440$. The number of complete cells within this area was then counted. Ashby's method was then used to calculate the total number of cells, adding to the number of whole cells a correcting number to take into account the cells which were only partly within the square. The average area of one cell was then calculated from the known area of the square and the corrected number of cells enclosed in this area. Before this method was adopted, the outlines of the cells were drawn by camera lucida and the area of the cells was calculated from direct measurements. It was found that there was a reasonable agreement between this method and that of Ashby but the latter method was felt to be more accurate and more rapid.

The shape and size of cells from different parts of the upper epidermis were compared. Cells along the mid-rib region are very narrow and elongated; otherwise there is no conspicuous difference in shape or size of cells from different parts of the leaf. Stomata are few in number and approximately the same size as epidermal cells. Also, it is often difficult to recognize them in peels. Therefore stomata, when they occurred in a field being examined, were counted as one cell. Consequently, counts of the number of cells in the measured area were made at random, only the midrib region being avoided.

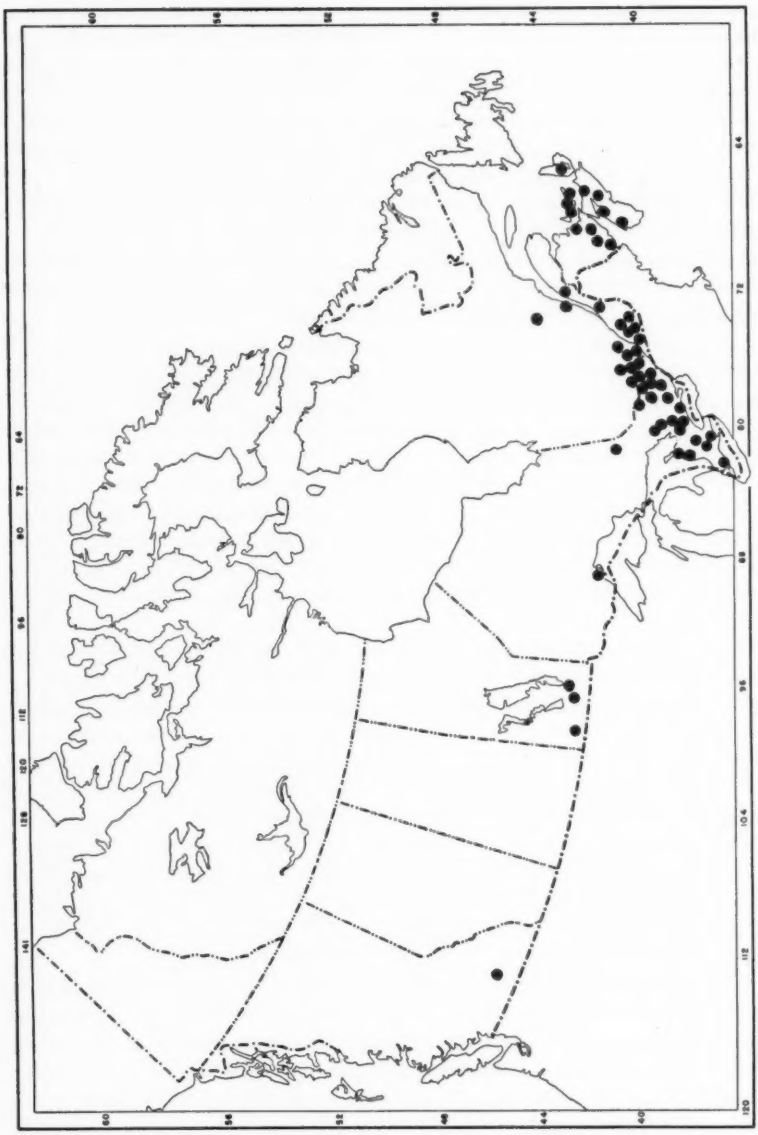


FIG. 1. Distribution of *Euphorbia cyparissias* L. in Canada.

Distribution of *Euphorbia cyparissias* L.

Euphorbia cyparissias L. as an indigenous plant is distributed through all central and southern Europe (10). The northern limit is reached in England (Cumberland Co.), Denmark, south and central Sweden, the Baltic States, and central Russia. The southern boundary is central Spain, southern Italy, Albania, Macedonia, and southern Russia. In the east, the species reaches to Lake Baikal in Siberia.

It is not known when *Euphorbia cyparissias* was brought to North America, but probably it was introduced not later than the middle of the nineteenth century. Gray (9) records that the species was found as an escape in New England in 1867. In the same year, Hubbert (11), in a catalogue of the plants of Canada, lists the species as an "occasional escape from cultivation about dwellings". In 1880, Fletcher (8) reports that the plant was to be found in the Ottawa district and, in 1883, Macoun (13) lists *Euphorbia cyparissias* as an escape at several points in Nova Scotia and New Brunswick and in southeastern and southwestern Ontario.

At the present time, cypress spurge is widespread in Eastern Canada. The distribution shown in Fig. 1 is based on specimen records from three herbaria. In most of the locations shown in Fig. 1 the amount of cypress spurge is very small. However, at some points in Eastern Canada very large areas are covered by the weed. Roland (17) noted a large stand at Mile River, N.S., and Barabé and Gagnon (3) described another serious infestation at Baie St. Paul, Que. Other large stands are known to be present at Charteris, Que., and Braeside, Port Hope, Galt, Bobcaygeon, and Goderich, Ont. (12). A large field of sterile cypress spurge at Goderich, Ont., is shown in Fig. 2. Some of these infestations cover several hundred acres. A fertile infestation at Braeside is scattered over approximately nine square miles and covers a total of some 300 acres of pasture and waste land in the area. Undoubtedly other large stands of the weed exist in eastern Canada but are as yet unreported.

Fertility of *Euphorbia cyparissias*

During weed surveys made over the past several years, it was observed that most of the stands of cypress spurge located in the Ottawa area appeared to be completely seed-sterile. These colonies were reproducing solely by the creeping rootstock and, unless spread by mechanical means, such as road grading or ploughing, remained as a single localized stand. On the other hand, it was noted that the more serious infestations at Braeside, Port Hope, Galt, and Bobcaygeon, Ont., and Baie St. Paul, Que., bore great quantities of seed.

There were two criteria which could be used in the field to distinguish between fertile and sterile stands. Firstly, the seed-producing stands occurred in patches: separated colonies were found scattered throughout the infested area, whereas sterile stands were largely confined to the point of original introduction and were continuous. However, the superficial appearance of a

stand may be deceptive, since sterile plants can be spread by the mechanical breaking of the rootstock. The second criterion was more reliable. It was observed that the male flowers of fertile plants were well-developed and strongly exserted from the cyathium whereas those of sterile plants were often rudimentary or absent. The common occurrence of sterility in the species was confirmed by the examination of herbarium material. Of some 60 specimens examined, it was found that only a few bore seed or well-developed male flowers. These fertile specimens had been collected from areas at which large fertile infestations are now known to exist.

The matter of rarity of seed production in cypress spurge has received considerable attention from other workers. Deane (5, 6) was able to record only three seed-producing stands in the United States and one in Canada after a 30-year search. He noted also that these fertile stands spread rapidly. Dymes (7) commented on the rarity of seed production by the species in England. Further reference to both fertile and sterile stands was made by Muenscher (15) who observed that most of the stands in New York State were obviously sterile but that a large infestation in one location bore abundant seed.

Chromosome Counts

The chromosome number of *Euphorbia cyparissias* L. has been reported as $2n = 20$ by Rutland (18) and by Perry (16). Examination of 22 plants collected in Eastern Ontario and adjacent Quebec showed that the chromosome

TABLE I

CHROMOSOME NUMBERS OF ONTARIO–QUEBEC COLLECTIONS OF *Euphorbia cyparissias* L.

Plant No.	Location of collection	Collector and date	$2n$	Fertility*
E-1	Near Gillies Lumber Co., Braeside, Ont.	D. Lindsay & I. Bassett, Sept. 1950	40	
E-2	Stittsville, Ont	D. Lindsay & I. Bassett, Sept. 1950	40	
E-3	Stittsville, Ont.	D. Lindsay & I. Bassett, Sept. 1950	20	
E-4	Braeside, Ont.	D. Lindsay & I. Bassett, Sept. 1950	40	F
E-5	2½ mi. N. of Bristol, Que.	D. Lindsay & I. Bassett, Sept. 1950	20	S
E-6	Charteris, Que.	D. Lindsay & I. Bassett, Sept. 1950	20	S
E-7	Charteris, Que.	D. Lindsay & I. Bassett, Sept. 1950	20	S
E-8	Braeside, Ont.	D. Lindsay & I. Bassett, Sept. 1950	40	F
E-14	2 mi. NW. of Arnprior, Ont.	R. Moore & D. Lindsay, June 22, 1951	40	F
E-15	1 mi. E. of Braeside, Ont.	R. Moore & D. Lindsay, June 22, 1951	40	F
E-16	1 mi. SE. of Arnprior, Ont.	R. Moore & D. Lindsay, June 22, 1951	40	F
E-17	3½ mi. SE. of Arnprior, Ont.	R. Moore & D. Lindsay, June 22, 1951	20	S
E-21	East of Cassburn, Ont.	R. Moore & D. Lindsay, June 26, 1951	20	S
E-22	½ mi. W. of Vankleek Hill, Ont.	R. Moore & D. Lindsay, June 26, 1951	20	S
E-23	½ mi. W. of Vankleek Hill, Ont.	R. Moore & D. Lindsay, June 26, 1951	20	S
E-24	2½ mi. N. of Russell, Ont.	R. Moore & D. Lindsay, June 26, 1951	20	S
E-25	1 mi. W. of Ardoch, Ont.	H. A. Senn 5599, July 1, 1951	20	S
E-26	1 mi. E. of Chiswick, Ont.	H. A. Senn 5574, July 1, 1951	20	S
E-27	2½ mi. N. of Vernon, Ont.	C. Frankton, K. Bragg, & R. Moore, July 13, 1951	20	S
E-28	1 mi. S. of Vernon, Ont.	C. Frankton, K. Bragg, & R. Moore, July 13, 1951	20	S
E-30	1 mi. W. of Salem, Ont.	H. A. Senn 5628, July 15, 1951	20	
E-31	2 mi NE. of Sangster, Ont.	H. A. Senn 5630, July 15, 1951	20	

* *Observed fertility in the field. F = fertile. S = sterile.*

PLATE I

FIG. 2. Infestation of *Euphorbia cyparissias* L. at Goderich, Ont.

number of 15 plants was $2n = 20$, of the remainder, $2n = 40$ (Figs. 5, 6). These collections are listed in Table I and are shown on the map (Fig. 3). Field observations had been made on the fertility of most of the stands from which these plants had been taken; these also are shown in Table I. It will be noted that the correlation is complete between the tetraploid condition and fertility and between the diploid condition and sterility.

Morphological Evidence of Polyploidy

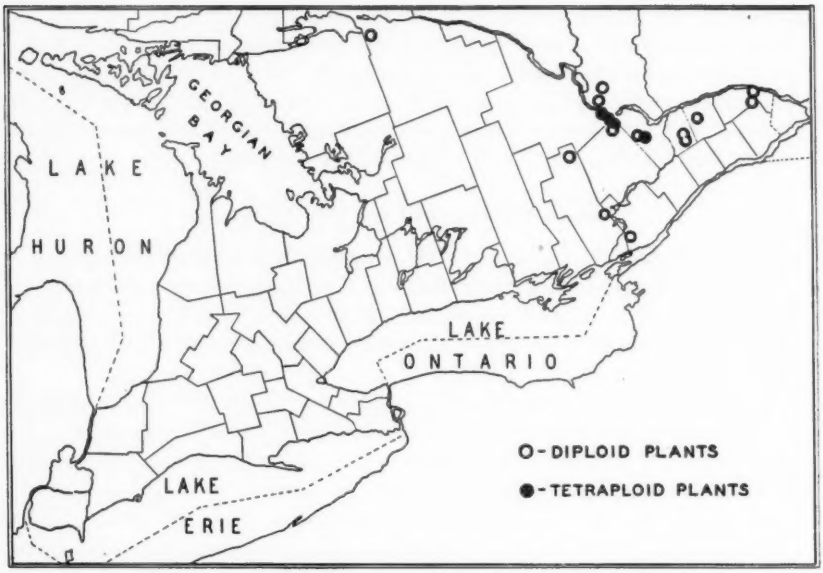
That polyploid plants consist of larger cells than do diploid plants is a well-known fact. Various morphological characters have been used as indicators of the polyploid condition—leaf thickness, pollen grain size, etc. Of special value are characters which can be easily measured on the ordinary herbarium specimen.

Size and frequency of leaf stomata (19, 20) and length of the guard cells of the stomata (2) have been successfully used as in index of polyploidy. In these studies, the stomata of polyploid plants were found to be larger and fewer in number per unit area of leaf surface than those of the diploid plants. The area of cells of the leaf epidermis was used by Burns (4) for the same purpose. The area of cells of octoploid species of *Saxifraga* was found to be approximately twice the area of those of tetraploid species.

Measurements of Leaf Cell Area

To determine whether or not the area of the cells of the upper epidermis of the leaf was correlated with the chromosome number, measurements were made on the leaves of the living plants for which the chromosome number was known. Cellulose acetate peels of the upper epidermis of mature leaves were used. Care was taken to select only mature leaves of normally growing plants. Young leaves or leaves from new growth from stunted plants will usually give a count lower than is normal for the plant.

In the case of herbarium specimens, peels made from dried leaves were compared with peels made from leaves which had been boiled. The epidermis of dried leaves was usually found to be wrinkled and the cells distorted and shrunken. Cell measurements showed that the area of cells of the dry leaf is appreciably smaller than the area of cells of the same leaf after boiling. The cells of boiled leaves were approximately the same size and shape as those of fresh leaves. Consequently, boiled leaves were used for measurements. To obtain an idea of the variation in cell size within one plant, measurements were made from several fresh, mature leaves and from several areas of each leaf of a diploid plant. It was found that in no case did the cell area at any point exceed the maximum allowed for diploid plants and the various measurements for different areas of one leaf did not depart from the average for that leaf by more than 10% of the average.



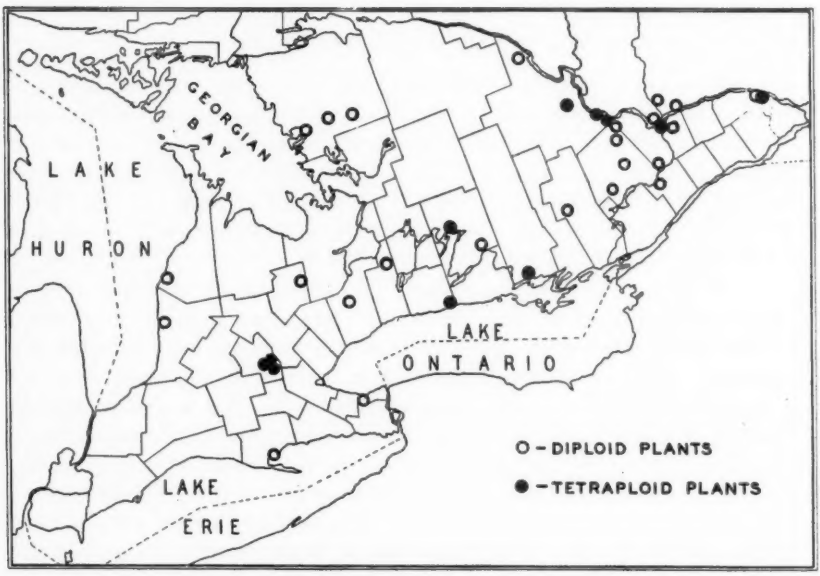


FIG. 3 (Top). Distribution of diploid and of tetraploid populations of *Euphorbia cyparissias* L. in Ontario, according to chromosome counts.

FIG. 4 (Bottom). Distribution of diploid and of tetraploid populations of *Euphorbia cyparissias* L. in Ontario, according to leaf cell measurements.

Cell area measurements for 17 of the living collections listed in Table I are presented diagrammatically in Fig. 8. With one exception, measurements for each plant are based on examinations of 8-10 fields of two to five fresh, mature leaves. Measurements for one collection were made from the herbarium specimen because the plant did not long survive transplanting. In Fig. 8 the plants are grouped according to their average cell areas in classes with a range of 50 μ^2, e.g. 400-450 μ^2, 451-500 μ^2. The number of plants in each class is shown on the ordinate, the average cell area on the abscissa. The 12 diploid plants lie in the area of the figure marked by horizontal shading, the five tetraploid plants within the area shaded vertically. From these measurements it was seen that there was a complete correlation between chromosome number and cell size: the cells of all the diploid plants were distinctly smaller than those of the tetraploid collections. After inspection of these data, the dividing line between the area of epidermal cells of diploid and of tetraploid plants was set arbitrarily at 650 μ^2, for use in the study of herbarium specimens. Plants with an average cell area greater than this figure were classed as tetraploid.

When this correlation had been established, it was decided to measure the cell area of herbarium specimens and thus attempt to class the specimen as diploid or tetraploid. In many cases, partly or wholly developed fruits were on the sheets; in others, the collector had recorded whether the planting had

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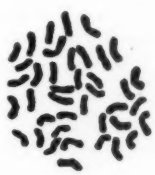

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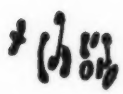

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FIGS. 5-7. Chromosomes of *Euphorbia cyparissias* L. × 2100.

FIG. 5. Somatic chromosomes of diploid plant (E-9).
FIG. 6. Somatic chromosomes of tetraploid plant (E-26).
FIG. 7. I meiotic metaphase of diploid plant (E-25).

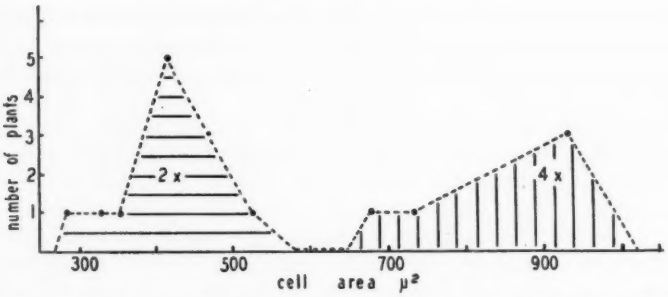


FIG. 8. Correlation between chromosome number and area of cells of leaf epidermis of living plants of *Euphorbia cyparissias* L.

been seed-sterile or not. Therefore it was possible to examine further the hypothesis that the diploid plants were sterile and the tetraploid fertile.

The result of the measurements of cell areas of the herbarium specimens from Southern Ontario is presented diagrammatically in Fig. 9. Specimens whose cell areas fall within the range marked by the horizontal shading were judged to be diploid; those which fell within the vertically shaded area were considered to be tetraploid. The distribution of these collections is shown in Fig. 4. The degree of polyploidy, as indicated by the cell area, is shown by the symbols used. Developing fruits were found on 5 of the 11 herbarium specimens judged to be tetraploid. It was not possible to state definitely whether the remainder were fertile or sterile, but the flowers of all appeared normal. No fruits were observed on any of the 25 specimens classed as diploids. In many of these specimens it was not possible, because of the age or flowering condition of the specimen, to form any conclusion regarding fertility.

It would be very interesting to learn whether or not the two chromosome numbers occur in Europe as well, and, if so, what is their range. The presence of diploids in Europe is shown by the two previous chromosome counts. The

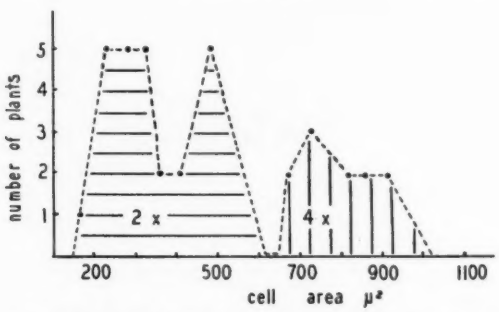
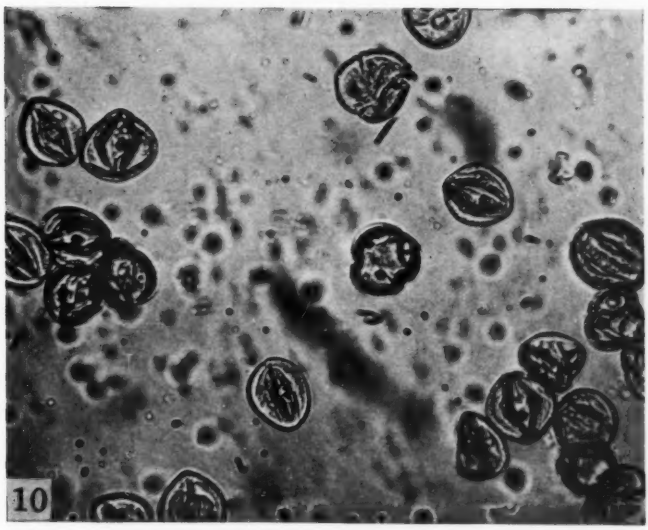


FIG. 9. Relationship between area of cells of leaf epidermis and presumed chromosome number of herbarium specimens of *Euphorbia cyparissias* L.



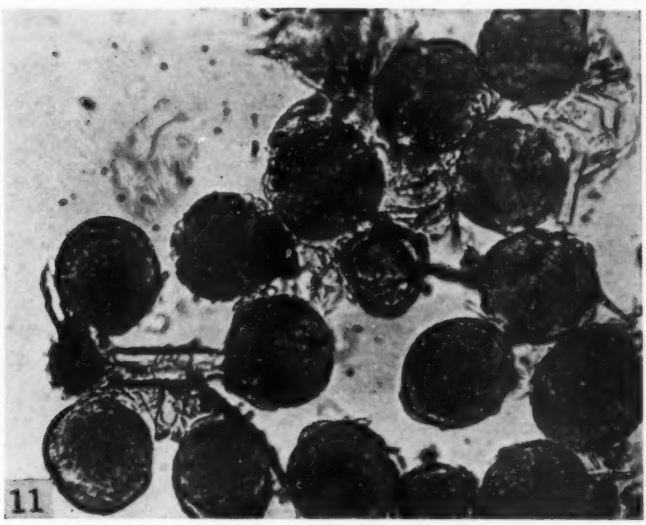


FIG. 10. Photomicrograph of pollen of sterile diploid plant. × 430.
FIG. 11. Photomicrograph of pollen of fertile tetraploid plant. × 430.

count made by Rutland was presumably made on local English material. The plant examined by Perry was obtained from a nursery in Virginia and was probably an imported ornamental. Perry made no observations on the fertility of the plant (private communication).

Only six European specimens were available in the herbarium at Ottawa. From an examination of the size of the epidermal cells, all would be classed as tetraploid. Four of these specimens were from Sweden, two from Finland. The occurrence of a tetraploid race, in northern Europe at least, is therefore suspected.

Meiosis and Condition of the Mature Pollen

It has been possible to study meiosis in only one diploid plant (E-25). The chromosomes are very small and analysis of meiotic configurations is difficult, but no meiotic irregularities could be detected. All I metaphase divisions were regular; 10 bivalents were formed (Fig. 7). Later stages of both the I and II meiotic divisions appeared normal and the tetrad cells were normal and uniform in size and shape.

The pollen of a small number of plants, the chromosome number and fertility of which were known, was examined in an attempt to gain a clue to the cause of the sterility. Without exception, the pollen grains of sterile diploid plants were uniform in size and shape, spherical, 22-26 μ in diameter (Fig. 10). So far as could be seen, the grains were completely empty and, consequently, non-functional. Pollen of tetraploid plants was more variable: large full grains 35-40 μ in diameter and a smaller number of empty grains 20-25 μ in diameter usually were found. A few of the grains with full protoplast are shown in Fig. 11. It has not been possible to examine the pollen of a sufficient number of tetraploid plants; the percentages of the good and of the empty grains varied widely in the counts made. However, the characteristic of the pollen of tetraploid plants was its variability in size and the presence of large full grains which presumably are functional.

Discussion

The cause of the seed-sterility of the diploid plants remains obscure.

Muenscher (14) reported that plants grown from one seed were sterile and that plantings established from several seeds were fertile. From this, he concluded that the plants were self-sterile because of self-incompatibility factors and plantings of one genotype would produce no seed. However, a stand composed of plants of genotypes different with regard to incompatibility factors would be fertile. Such a genetic system of self-incompatibility factors is well-known in many plants and may be the cause of sterility in some populations of this species. In such cases, pollen is functional only on pistils carrying at least one incompatibility allele different from the incompatibility allele carried by the pollen. Cross-pollination between different plants is therefore

essential. Apparently this explanation does not cover the whole situation in *Euphorbia cyparissias*. According to this hypothesis, the pollen of self-sterile plants would be normal. This is not the case in our sterile diploid plants: the pollen of all diploid plants examined was abortive. It seems certain therefore that populations composed wholly of plants with genetically abortive pollen would be sterile following either self- or cross-pollination.

Meiotic irregularities are frequently the cause of sterility. The observed regularity of meiosis in one sterile diploid plant indicates that this is not the case here. The possibility of interspecific hybridity, often the cause of irregularities in chromosome pairing, is also probably eliminated. Meiotic irregularities usually result in the formation of pollen grains of varying shapes and sizes. The uniform size of the empty pollen grains of the other diploid plants suggests that meiosis is regular in them also.

It may next be suggested that a genic condition which interrupts the normal pollen development is responsible for the sterility. Such a gene or gene complex would prevent the normal development of the pollen, possibly by interrupting the flow of nutrient material to the otherwise normal grains. As a result, the protoplast would soon die, producing the empty grains seen in the sterile diploid plants.

It is possible that horticulturists have selected sterile forms of *Euphorbia cyparissias* for cultivation, perhaps for their sterility or for some superior feature of their appearance or for their vegetative vigor. Such a clone or clones would doubtless have been extensively propagated, both by nurseries and by individuals who purchased the plant and thus could very easily have become widespread.

Whether or not the sterility of the diploid populations is peculiar to North American plants is an interesting question. Continental European literature does not mention the fertility of the species. This, of course, may merely reflect a lack of interest in this species, but quite possibly the species is normally fertile. Sterile clones may exist in Europe, but since they have not been propagated by man, are not sufficiently extensive to attract attention.

It is possible that diploid, as well as tetraploid plants free of the sterility gene may have been introduced into North America. Such fertile diploid plants have not yet been found in our region. The nature of the genetic fertility mechanism in the species is unknown. Diploid and tetraploid plants which are free of the gene for pollen abortion may both be self-fertile, or may be self-sterile and set seed only when pollinated by a plant of a different genotype. The diploid plants may be self-incompatible while the tetraploid plants may be self-compatible. There is room for an interesting investigation of the fertility of this species.

The complete correlation between the diploid chromosome number and sterility in Ontario suggests that such a sterility gene must be present in practically all our diploid populations and absent from the tetraploid populations.

Acknowledgments

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PHYLOGENY OF *CAREX* IN THE LIGHT OF PARASITISM BY THE SMUT FUNGI[1]

By D. B. O. Savile[2] and J. A. Calder[2]

Abstract

By using evidence derived from the relationships with smut fungi (*Cintractia* and *Planetella*) that attack its members, new light has been shed on the phylogeny of *Carex*. The genus is believed to be essentially monophyletic and derived from *Kobresia*. It has been found necessary to erect a new subgenus, *Kuekenthalia*, composed principally of those sections with persistent styles and bladdery perigynia that were formerly placed in *Eucarex*. *Uncinia* is shown to be an offshoot of the evolutionary line that gave rise to *Kuekenthalia*.

Introduction

Savile (8) recently completed a study of a group of smuts (*Cintractia* spp.) attacking *Carex*, *Kobresia*, and *Scirpus*, in which the phylogeny of *Carex* was considered very briefly. Soon afterward the stimulating discussion by Nelmes (6) on the phylogeny of *Primocarex* appeared, making it advisable to consider the evidence derived from the smut fungi in greater detail. Nelmes believes the subgenus *Primocarex* as constituted by Kükenthal (4) to be polyphyletic, with its species derived, generally with considerable reduction, from *Carex*, *Kobresia*, *Schoenoxiphium*, and *Uncinia*.

The presumptive contribution from *Schoenoxiphium* is limited to one Caucasian and a few Brazilian species, on none of which have smuts been seen. Several smutted sedges have been studied from each of Nelmes' other three *Primocarex* groups. The host distribution table for North America (8) and a substantial number of available European specimens combine to show that *Cintractia carpophila* and *Cint. caricis* (*sensu stricto*) occur in all three groups, and *Cint. limosa* in those allegedly derived from *Carex* and *Uncinia*. When the several varieties of these smuts are considered the duplication is even more impressive.

The species and variety concepts employed in the study of these smuts have an exacting morphological basis. It is accordingly believed that the taxa used are essentially natural and that the smut relationships provide a biochemical tool of real significance. The data must, of course, be used with some discretion. Many species of *Carex* take more than one smut, and incomplete data may therefore give erroneous impressions of relationship. Moreover, infection is doubtless partly controlled by the germinability of the smut spores when the potential host is in anthesis, by proximity to heavily infected sedges and possibly by other physical factors. Nevertheless, the trends indicated by a large body of data certainly cannot be ignored.

In view of the smut records it is difficult to believe that the three *Primocarex* groups in question are actually of completely diverse origin and their resem-

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blances due only to convergent evolution; in fact, there seems to be almost as much diversity within as between them. Smut records are almost entirely lacking for the predominantly tropical groups, but they cover a substantial proportion of boreal species. As far as the latter are concerned the smut data suggest that *Carex* in the broad sense is a reasonably natural genus within which several divergent lines of evolution have been active.

Basis of Proposed Phylogenetic Arrangement

The following phylogenetic principles are pertinent to the Caricoideae:—

(1) Within a simple evolutionary series the evolutionary trend of any character will not be reversed unless a change in external conditions makes such a change advantageous. This point will be discussed further in the last section.

(2) Evolution is from free to connate parts. Thus the perigynium of *Carex* or *Uncinia* is more advanced than the partly fused floral bract of *Kobresia* or *Schoenoxiphium*.

(3) Complex flowers and inflorescences give way eventually to simple. Thus the bisexual spikelet of some species of *Kobresia* or *Schoenoxiphium* is succeeded by the simple pistillate floret, at first with the rachilla that bore the staminate floret and eventually without it, provided that the rachilla attains no new function. Similarly the complex inflorescence tends to become reduced to a single spike; but, although this reduction has been evident repeatedly in the Caricoideae, the tendency is weak or absent in some groups that are advanced in all other respects. We must not derive a species with several spikes from one with a single spike. Nevertheless, the simplified inflorescence is not by itself sufficient evidence to justify placing a group in an advanced position. *Primocarex*, as here delimited, is plainly primitive in its possession of a rachilla and tristigmatic floret and in the resemblance of some species to *Kobresia*, although the present species have solitary spikes. It is believed that *Carex* as a whole is derived from *Primocarices* with several spikes and that reduction of the inflorescence has proceeded further in this ancient group than in the various groups derived from it.

(4) Flowers with many parts give way to those with few parts. Although this rule gives us the direction of evolution, it is of little aid in indicating relationship. The reduction from tristigmatic to distigmatic florets has occurred repeatedly in the subfamily, and both types of floret may be found in the same section, e.g. *Atratae*, *Vesicariae*, and *Foetidae* as the last-named section is here defined.

(5) In any attempt to arrange a group of organisms in phylogenetic sequence, one may expect to find conflicting indications of relationship and have to explain some of the resemblances by convergent evolution. The phenomenon of convergent evolution is more widespread than is sometimes realized, many quite startling examples occurring throughout the plant and animal kingdoms. When trying to decide which of two conflicting resemblances is attributable to relationship and which to convergent evolution,

one must consider the likelihood of a character being independently derived on two or more occasions. For example, the form of the ostiole of the perigynium generally is of little obvious importance in the success of a species, although the bifid form may sometimes aid in dispersal. Within the limits imposed by the morphology of the bract from which the perigynium is derived, we may expect the ostiole to be entire, dorsally cleft or oblique, or bifid. That all these forms occur repeatedly in the subfamily Caricoideae need not surprise us, and we can place little reliance upon ostiole shape as a guide to phylogeny. Similarly the inflorescence can only remain compound or become reduced, and, with such limited choice, its form cannot be regarded as of great significance. In contrast, characters such as the possession of a rachilla, or of the rigid, unjointed, persistent style found in the *Vesicariae* and related sections seem to be of fundamental importance. The former can only be regarded as the relic of a staminate floret and must indicate some degree of relationship unless *Carex* is regarded as polyphyletic. The latter is a striking character and, since it is correlated with well-defined perigynial characters, appears to be of considerable significance.

(6) New evolutionary lines spring from unspecialized groups of great genetic plasticity, not from specialized, climax groups. The classic example is the origin of various dicotyledons and the monocotyledons from the Ranales. This principle makes it difficult to believe that *Uncinia* could have given rise to the section *Unciniaeformes*, whose origin is more logically to be sought in *Kobresia* or a kobresia-like *Primocarex*.

It is next necessary to consider the species of *Cintractia* attacking *Carex* and *Kobresia* in order to assess the value of the data derived from them. *Cintractia carpophila*, in its four varieties, is beyond reasonable doubt the basic species of the group attacking *Carex*. It occurs most abundantly in *Kobresia*, true *Primocarex*, and *Vignea*, but also sparingly in *Eucarex* and the new subgenus described below. No other species has this wide host range. *Cint. carpophila* has small, rounded spores, and spore walls with little sculpturing but usually several well-defined internal swellings. These swellings are most marked in immature spores, and, in keeping with Haeckel's principle that ontogeny recapitulates phylogeny, are regarded as a primitive character. As already indicated (8), the remaining smuts in this complex have evidently developed from a form close to *Cint. carpophila*, with increasing size, angularity, or verrucosity of the spores.

If *Cintractia carpophila* is accepted as the basic member of the group of smuts with which we are concerned, we must regard it as originating in *Kobresia*, spreading through *Primocarex* and the other subgenera, and reaching its greatest development in *Vignea*. It was pointed out previously that the two main groups arising from *Cint. carpophila* (one comprising *Cint. aspera*, *Cint. fischeri* and *Cint. subinclusa*, and the other *Cint. caricis* and related forms) indicated two evolutionary lines within the host plants; but no attempt was made at that time to discover the point at which these lines diverged. As will be shown later, it is now evident that the *Vesicariae* and related sections with

bladdery perigynia are derived from *Primocarex* quite independently of the other *Eucarex* sections and must be placed in a new subgenus. Almost all the more advanced members of this subgenus are paludal, and it now becomes clear that the high, crowded, more or less cylindrical warts of *Cint. aspera*, *Cint fischeri*, and *Cint. subinclusa* are an adaptation to bog or marsh habitats where the ground is generally inundated at least in early summer. It is clearly advantageous that spores in such habitats should float indefinitely, both as an aid to dispersal and to allow germination when the host is in anthesis. The close-set warts must trap air bubbles effectively and add greatly to the buoyancy of the spores. *Cint. subinclusa*, in which the warts tend to spread out laterally at the apex (8, Fig. 2) shows this adaptation to the paludal habitat in greatest degree. These three smuts have been recorded on marsh- and bog-inhabiting species of *Vignea* or the groups removed from *Eucarex;* but never on species of *Eucarex* as it is here delimited, although a number of the latter occur in similar habitats and take other smuts. It is accordingly believed that the new subgenus is more closely related to *Vignea* than to *Eucarex*.

The resemblances of certain *Primocarices* to other genera indicated by Nelmes are in some instances striking, and there can be little doubt that *Primocarex*, as Kükenthal delimited it, is a mixture of primitive and reduced forms. In attempting to reconcile Nelmes' points of resemblance with the smut evidence, use has been made of the cytogenetic data of Heilborn (2, 3) and Wahl (9), as well as morphological and distributional clues. The cytogenetic data are of limited value, and must continue to be until chromosome counts are available in some quantity for the true, rachilla-bearing *Primocarices* and for *Uncinia*, *Kobresia*, and *Schoenoxiphium*. Nevertheless, several clues were obtained from Heilborn (2), notably the basic position of the *Montanae* within *Eucarex*, and the trend from low, terrestrial to tall, aquatic habit in two evolutionary lines ending in sects. *Acutae* and *Vesicariae*. The latter suggestion complements the clear indication of two divergent evolutionary lines in the smuts attacking these two groups. Heilhorn's suggestion that the *Montanae* may be an unnatural section cannot, however, be sustained. The few smuts seen on European *Carex pilulifera* and *C. montana* are in the same group of intergrading varieties of *Cintractia caricis* as those attacking various *Montanae* in North America; and morphologically the section appears quite homogeneous. The smut data, the clues from Heilborn, a consideration of dispersal mechanisms, various morphological considerations, and the assumption that simplification of both inflorescence and floret have occurred independently several times have led to an evolutionary scheme that meets the most important of Nelmes' postulated resemblances while overcoming several difficulties attendant on the acceptance of his arrangement. This scheme, shown diagrammatically in Fig. 1, is believed to be substantially more natural than any hitherto presented. It is far from complete, relying as it does to a considerable extent on the boreal species, but it is thought advisable to present it as a basis for further work. Space does not permit the definition of the

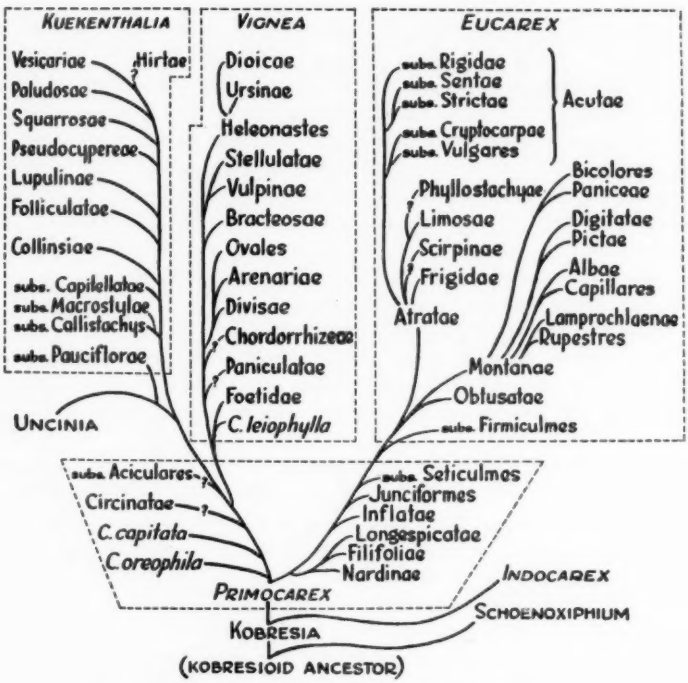

FIG. 1. Evolutionary diagram of the subfamily CARICOIDEAE: approximately complete for *Kuekenthalia* and *Primocarex* only.

sections and subsections included in Fig. 1, but the more advanced groups are largely according to the usage of Mackenzie (5) and the more primitive mainly according to Kükenthal (4). Some exceptions are discussed in the text.

It will be seen from Fig. 1 that all the subgenera of *Carex* are derived from *Kobresia* and that *Uncinia* is regarded as a specialized side branch from one of the several evolutionary lines. It is open to argument whether *Schoenoxiphium* has been derived from *Kobresia* or whether both have originated from a common ancestor. Similar evolutionary sequences occur in each genus; and some characters, such as a flattened, serrate rachilla, are shared by certain species of both genera and of *Primocarex*. Complex new groups may be expected to arise from unspecialized ancestral forms of great genetic plasticity. It is, therefore, reasonable to assume that the genetic potentiality for these shared characters was present in the presumptive kobresioid ancestor. Accordingly, although the resemblances of particular species of *Kobresia* to *Carices* of different divergent lines might be taken as evidence that the subgenera of

Carex have arisen independently within *Kobresia*, it seems advisable to assume a strictly monophyletic origin unless convincing evidence to the contrary is presented. In any case, the alternative would involve raising the subgenera to generic rank, which is impractical at present with the subgeneric affinities of numerous species still in doubt.

Primocarex

Primocarex, as here treated, includes 27 of the 60 species assigned to it by Kükenthal and a few described since, e.g. in sect. *Filifoliae*; and 30 have been assigned to other subgenera. No disposition has been made for *Carex grallatoria*, *C. leptalea*, or *Cymophyllus fraseri*. The species left in *Primocarex* are plainly primitive in the possession of a rachilla and, in some instances, a marked resemblance to individual species of *Kobresia*, although the inflorescences are reduced. There has been a tendency to place some *Primocarices* in *Kobresia*; but this practice seems undesirable, since the presence or absence of a completely fused perigynium is the most reliable character for distinguishing between *Carex* and *Kobresia*. If any species with fully developed perigynia are placed in *Kobresia* the boundary between the genera becomes extremely vague. In any event, of the species that Nelmes assigns to *Kobresia*, *Carex obtusata* and *C. rupestris* show affinity to the *Montanae* in their smut relationship. The latter is here regarded as reduced from the *Montanae*, but the former, because of its rudimentary rachilla, is presumed to have branched off lower in the same line.

Indocarex

The point at which *Indocarex* diverges is doubtful. It has been placed low down because the complex inflorescences and uniformly tristigmatic pistillate florets suggest that it is relatively primitive. Lack of data preclude any attempt to indicate evolution within this subgenus at present.

Eucarex

The tentative evolution of some sections and subsections of *Eucarex* is shown in the diagram, partly on the basis of smut relationship. Sects. *Obtusatae* and *Firmiculmes*, with most species having rudimentary rachillas, might be placed high in *Primocarex* or low in *Eucarex*. They are here included in *Eucarex* mainly because of their smut relationships, but further smut records from typical *Primocarices* might necessitate a change. The *Montanae* have low chromosome numbers and, as Heilborn deduced, appear to be the point of origin of several sections, some complex in structure and others markedly reduced. Many species in these sections take smuts indistinguishable from those attacking *Montanae*.

Sect. *Atratae* appears to require division into subsections. As the smut records indicate, *Carex atrata*, *C. podocarpa*, and *C. raynoldsii* are closely linked, but other species are diverse in their smut relationships. If the section is natural it appears, from morphological, cytogenetic, and smut data, to be

the starting point for sects. *Frigidae* and *Acutae*, and perhaps *Phyllostachyae*, *Limosae*, and *Scirpinae*. *Phyllostachyae* and *Scirpinae* are considered to be reduced rather than primitive because their smuts are advanced and related to those of *Limosae*. It seems advisable to follow Kükenthal in making *Cryptocarpae* a subsection of *Acutae*, for, as already indicated (8), they and *Vulgares* show closer affinity than do *Vulgares* and some other subsections.

It will be seen that several sections have been removed from *Eucarex* and placed in a new subgenus. This group is tentatively derived from the same evolutionary line as *Vignea*, because several hosts in sects. *Chordorrhizae*, *Paniculatae*, and *Heleonastes* take *Cintractia fischeri*, a smut common on species of *Vesicariae*, although the majority take *Cint. carpophila*, the principal smut of *Vignea*.

Vignea

Although *Vignea* is essentially a natural subgenus, the distinctions between sections are often small and the arrangement shown is decidedly hypothetical. It has already been shown (7) that *Carex maritima* and *C. leiophylla* are the only known hosts for a very distinctive smut, *Planatella lironis*. In view of the writers having scrutinized some 2000 collections of *Carex*, many of them large, from northern Canada and Alaska, in addition to searching for *Carex* smuts in the field, the finding of this smut only on these two remarkably similar species can hardly be ascribed to chance. *C. leiophylla* is evidently a nearly direct ancestor of *C. maritima* and should be placed in the same section as the latter although it is tristigmatic. For the present the authors are placing *C. leiophylla* with sect. *Foetidae* (as delimited by Mackenzie) in *Vignea*, in preference to placing *C. leiophylla* in *Eucarex* and regarding the species of *Foetidae* as reduced members of that subgenus. There seems to be no valid objection to deriving the *Foetidae*, with perigynia having dorsally cleft ostioles, from a species with bifid ostioles; for oblique or dorsally cleft ostioles occur sporadically in *Primocarex*, *Indocarex*, *Eucarex*, and *Vignea*, and seem to have evolved independently several times. It is hoped that *Cintractia* specimens will eventually be obtained on species of *Foetidae*, which may indicate their true affinities more clearly.

The arrangement of the remaining sections of *Vignea* that have been included in the diagram is based mainly on morphological and cytogenetic data. Although *Cint. fischeri*, a smut generally found on members of the next subgenus, is found on species of sects. *Chordorrhizae*, *Paniculatae*, and *Arenariae*, we find no justification for basing a division within *Vignea* on these smut records. The occurrence of *Cint. fischeri* does suggest that *Vignea* is closer to the next subgenus than to *Eucarex*, in which this smut is not known to occur; but, as noted above, its occurrence in these particular sections is probably a reflection of the marsh or bog habitats of the hosts.

Heilborn (2) indicated that the *Dioicae* should be in the *Vignea*. Our smut and natural hybrid records for *C. gynocrates* confirm this viewpoint and suggest that the section represents a reduction from the *Heleonastes*. A single smut

specimen (aff. *Cint. pratensis*) on *C. exilis* suggests that this species was incorrectly placed in sect. *Stellulatae* by Mackenzie (5) and Fernald (1). Kükenthal's disposition of it in sect. *Dioicae* may prove to be more natural. Although *C. gynocrates* generally takes *Cint. carpophila*, one collection upon it is referable to *Cint. limosa*, a smut related to *Cint. pratensis* and, like it, occurring mainly on species of *Eucarex*; and *C. dioica* in Europe take an imperfectly understood series of smuts very similar in morphology.

C. ursina, which has no rachilla, is tentatively regarded as a reduced member of the *Heleonastes*.

Kuekenthalia

We now come to an interesting series of plants for which it is necessary to erect a new subgenus, named in honor of Georg Kükenthal, monographer of the Caricoideae in *Das Pflanzenreich:*

Kuekenthalia Savile & Calder subgen. nov.

Perigynia matura a valde divaricatis, deflexa, lanceolato subulata vel conspicue inflata; stylus firmus et marcescens; stigmata saepius tria; achaenia saepius trigona.

Species typica: *Carex vesicaria* L.

Evolution in *Kuekenthalia* has been governed largely by the development of seed dispersal mechanisms. The group has arisen from an evolutionary line with pronounced kobresioid affinities, in which the rachilla was well-developed, but evidently not strongly flattened, and perhaps bore a staminate floret. The ancestral form had slender, subulate, divergent perigynia and may have resembled *Kobresia laxa* in many respects. The slender, divergent, and readily detached perigynia constituted an elementary mechanism for dispersal by animals, somewhat akin to that of *Hystrix patula* in the grasses and sufficiently effective to stimulate further developments of the mechanism. All the obvious modifications and improvements may be seen in the species derived from the ancestral form. The most primitive sedges clearly assignable to *Kuekenthalia* among living species are those in the subsections *Capitellatae*, *Callistachys*, *Macrostylae*, and *Pauciflorae* of sect. *Unciniaeformes*, but all of these have reduced inflorescences and cannot be considered as being on the direct evolutionary line. Subsect. *Aciculares* and sect. *Circinatae* seem to have diverged from lower on the *Vignea-Kuekenthalia* line and are, perhaps, best left in *Primocarex*.

Carex pyrenaica (Subsect. *Callistachys*) is probably close to the first representatives of *Kuekenthalia* in the form and disposition of its perigynia. The more advanced, distigmatic species of subsect. *Macrostylae* show perhaps a slightly improved dispersal mechanism in their somewhat more strongly deflexed perigynia. When the culms of such plants are bent over by a passing animal the perigynia point backward and are easily thrust deeply into its fur, increasing the probability both of their breaking off and of their being carried a substantial distance. In subsect. *Pauciflorae* the same dispersal mechanism is even more highly developed. It is difficult to secure good specimens of

C. microglochin and *C. pauciflora* because, like *C. pyrenaica*, their perigynia detach at a touch a few days after becoming reflexed. Both species have long-pointed, extremely slender perigynia that penetrate fur very readily. In *C. microglochin* dispersal is possibly aided somewhat further by the slender, projecting rachilla. *C. microglochin*, as Nelmes maintains, provides the connecting link with *Uncinia*, but the direction of evolution cannot well be in the direction that he postulates. The only satisfactory solution seems to be to regard *Uncinia* and the *Pauciflorae* as diverging from a common stock.

Two obvious evolutionary courses are open to the rachilla in a species like *C. microglochin*. If it attains no well-defined function it will tend to degenerate, and once it is included in the perigynium, degeneration is virtually certain: thus we get the *microglochin–parva–pauciflora* sequence. If, however, the rachilla chances to develop a curved or irregular tip that enhances the tendency of the perigynium to lodge in an animal's fur, then we may expect its elongation and development into a hook like that of *Uncinia*. In most species of *Uncinia* of which specimens or adequate illustrations are available the tip of the hook flares outward, but at the bend the gap is very narrow. Such a hook is extremely efficient for jamming on hairs or feather barbs between which it has been thrust. This hook is a highly specialized device; and *Uncinia*, despite its tristigmatic florets, is a relatively advanced genus with completely closed perigynia. As such, it is a most improbable starting point for a new group of plants such as the *Unciniaeformes*. The evolutionary scheme here presented overcomes three other difficulties involved in Nelmes' interpretation, in addition to that of the smut data. First, as Nelmes admits, it would be astonishing if so efficient an organ as the hook of *Uncinia* had degenerated without evident cause. Second, it is not in accord with phylogenetic principles that the direction of evolution should be abruptly reversed in a simple evolutionary series, which would be necessary if *Uncinia* developed from a hypothetical hookless ancestor and later gave rise to the *Pauciflorae*. Finally, there exists, to the best of our knowledge, no evidence of such a hypothetical ancestor; for *U. kingii* cannot be both a primitive *Uncinia* and, as Nelmes regarded it, a step from *Uncinia* toward *C. microglochin*.

Returning to the main line of development we find in sect. *Collinsiae*, represented by the single species *C. collinsii*, a further modification of the mechanism for dispersal by animals. The subulate, divergent to deflexed perigynia have slender ostiolar teeth that reflex abruptly at maturity to provide narrow, retrorse hooks about 0.5–1.0 mm. long. From *C. collinsii* we have a well-defined series through the *Folliculatae* and *Lupulinae* to the prevailingly aquatic species of sects. *Hispidae*, *Pseudocypereae*, *Squarrosae*, *Paludosae*, and *Vesicariae*, with inflated perigynia. Sect. *Hirtae* is tentatively added to this group on the basis of perigynium shape and the susceptibility of some species to *Cintractia fischeri* and *Cint. subinclusa*, which attack species of *Vesicariae*, *Paludosae*, and *Lupulinae*. It may be noted that, in addition to

the North American records, there are various European records of *Cint. subinclusa* on *Carex lasiocarpa*. It is also noteworthy that the seven intersectional hybrids listed by Kükenthal for species of *Hirtae* are all with species of *Vesicariae* or *Paludosae*. On the other hand the smuts examined on *C. hirta*, a dry-land species, have proved to be *Cint. caricis* and *Cint. irregularis*, two species almost exclusively associated with *Eucarex*. Both the smut records and the hybrids are conceivably due to frequent association with species of *Kuekenthalia*; but in that event we would expect species of, e.g., *Acutae* to hybridize with species of *Hirtae* and to take *Cint. fischeri* and *Cint. subinclusa*. The most probable explanation seems to be that sect. *Hirtae* was derived from hybridization between species of *Kuekenthalia* and *Eucarex* and subsequent amphidiploidy. The rather high chromosome counts reported in the section ($n = 39$ and 60) lend some support to this explanation, for doubling might well be essential to fertility in such hybrids.

It might be argued that it is as inadmissable to postulate the degeneration of a mechanism for dispersal by animals in *Kuekenthalia* as in *Uncinia*; but the explanation lies in the change to an aquatic habitat in which such a mechanism would be almost valueless. Thus, with the adoption of an aquatic habitat, we see the slender perigynium give way in the higher sections of *Kuekenthalia* to a bladdery pergynium adapted to dispersal by water. The few terrestrial species in these sections are evidently secondarily so. The relatively high proportion of terrestrial species in sect. *Hirtae* is perhaps further evidence of the hybrid origin of this section.

After this manuscript was submitted specimens of *Cintractia sclerotiformis* on *Uncinia leptostachya*, *U. riparia*, and *U. rubra* were received through the courtesy of Miss Shirley D. Baker, Plant Diseases Division, New Zealand Department of Scientific and Industrial Research. The spores of this smut are usually conspicuously angular or irregular, although the walls are finely verrucose or almost smooth and internal swellings are developed to some extent. The spore shape clearly indicates that it is more advanced than *Cintractia carpophila*. It must be concluded that *Cint. carpophila*, attacking *Carex microglochin*, cannot have been derived from *Cint. sclerotiformis* although the converse is quite possible. The morphology of *Cint. sclerotiformis* thus offers slight additional evidence that evolution of *Uncinia* and *Carex* sect. *Unciniaeformes* has been in the direction proposed above.

Acknowledgments

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STUDIES IN FOREST PATHOLOGY

X. DECAY OF WHITE PINE IN THE TIMAGAMI LAKE AND OTTAWA VALLEY AREAS[1]

L. T. WHITE[2]

Abstract

The study of decay and decay relationships of white pine was undertaken to provide forest authorities in Ontario with information essential to the management of even-aged stands. Of 1012 white pine trees examined in 10 1-acre plots, located in even-aged white pine stands, 52% contained decay. A well-defined relationship existed between age and decay. The proportion of trees with decay increased gradually with age from 40% in the 60-year age class to 100% in the 220-year age class. The loss in merchantable volume increased from 4% at 60 years to 40% at 200 years. No consistent relationship between percentage of decay and diameter was found. The incidence of decay in vigorous and non-vigorous trees was about the same but the percentage of volume lost through decay was considerably higher in slow-growing, less vigorous trees. The pathological rotation, as indicated by the maximum periodic increment, was 160 to 170 years. A number of methods of estimating the volume of decay in logs are compared. Regression lines, which define the percentage of cull allowances at all ages, are presented. Thirteen wood-destroying fungi were found to be associated with the decay of living white pine in Ontario. *Fomes pini* (Thore) Lloyd was responsible for 90% of all loss in trunks and butts of living trees. External signs of decay were rare, except in cases of advanced white pocket rot caused by *F. pini*.

Introduction

For many years white pine furnished the best known and most highly regarded lumber on the North American continent and, prior to 1900, led among the saw timbers in Canada in quantity cut. It is estimated that at the height of white pine logging over 1,000,000,000 ft. b.m. were cut each year in the Ottawa Valley alone. Heavy inroads were made into the white pine resources. Although today white pine occupies only fourth place in Canadian lumber production, the annual cut is over 375,000,000 ft. b.m. (2).

In Ontario, white pine (*Pinus strobus* L.) occupies a prominent place in the forest economy. Nearly 75% of the available merchantable white and red pine (*Pinus resinosa* Ait.) in Eastern Canada occurs in this province (6,100,000,000 ft. b.m.) (1). Approximately 85% of this amount is white pine. During 1950, white pine lumber constituted more than one-quarter of all the lumber sawed in Ontario. The amount exceeded 220,000,000 ft. b.m. (3).

If white pine is to remain an important source of timber in Ontario adequate management plans will be required. A knowledge of disease relationships and pathological rotation ages is essential for such plans.

At present the major part of commercial cutting of white pine in Ontario is located in overmature stands. These had been reported to contain abnormal

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Contribution No. 68 from the Division of Forest Biology, Science Service, Department of Agriculture, Ottawa, Canada. Based on part of a thesis presented in April, 1950, to the University of Toronto in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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volumes of defect and a number of requests were received from the logging industry and the Ontario Department of Lands and Forests for information about the decay losses in white pine. Pathological investigations to determine the relationship between disease and tree age, diameter, site, and other factors were regarded as matters of urgency by representatives of industry and by the Provincial Forest Service.

Since no published data were found to pertain to this problem an investigation was begun during the summer of 1947 and continued through two field seasons. This paper reports the findings of that work.

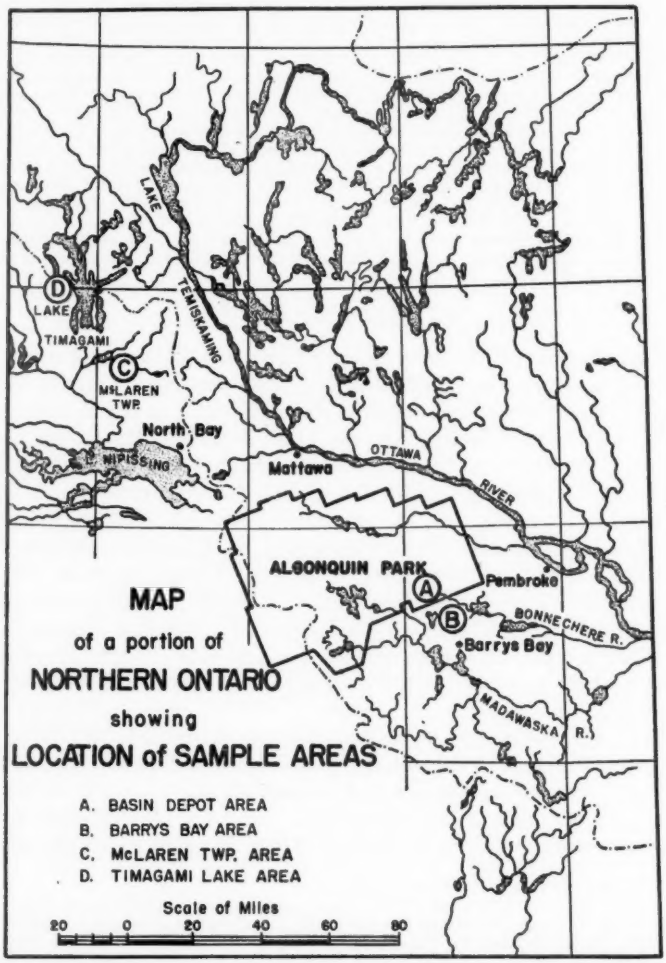


FIG. 1. Map of a portion of Ontario showing the location of study areas.

Location of Study

The studies outlined herein were conducted in four regions which supported white pine stands. These were chosen to represent typical age classes and at the same time to give an adequate area coverage. Areas were located as follows:

1 acre about two miles west of the Basin Depot in Algonquin Park;
3 acres in Burns Township, south of Algonquin Park;
2 acres at Holdridge Creek in McLaren Township within the limits held by the Gillies Lumber Company;
4 acres on an operation of the Wm. Milne & Sons Limited in the Timagami Lake area.

Method of Study

One-acre sample plots were used as the basic areas in this study. In order to obtain uniform composition and to avoid local variations in terrain, the plots were organized in ¼ ac. units. These units were always contiguous, but the shape of the acre plot was not always square.

The living white pines on the plots were felled, bucked into logs, and examined for decay. The plots were clear cut to the following minimum diameter limits:

Mature and overmature stands — 12 in. d.b.h.
Younger stands (in some cases) — 6 in. d.b.h.

All logs from trees of sawlog size were scaled from the point at which they were cut to a minimum top diameter of eight inches. Stump heights varied from six inches to two feet. Scaling was carried out in conformity with the *Manual of Scaling Instructions* (third edition) published by the Ontario Department of Lands and Forests. The volumes of logs were measured in board feet according to the Ontario Log Rule.

In 1947 the Report of the Ontario Royal Commission on Forestry (4) recommended that all wood, whether logs or bolts, be measured on a cubic measurement basis. In recognition of this proposal merchantable white pine logs were scaled in cubic feet. Several methods of deriving the cubic foot volumes of merchantable logs, and the contained decay, were tested to determine their efficiency.

Absolute relationships existing between total tree volumes and decay volumes were investigated. Total cubic volume tables were prepared to illustrate these relationships.

The stump age of each tree was determined. In cases where a large amount of butt rot made complete ring counts impossible, ages were considered comparable to those of adjacent trees of similar diameter and ring pattern. Since all plots were established in even-aged stands, the age spread among these trees was not excessive. Total ages were derived by adding the number of years it took these trees to grow to the measured stump heights.*

* *Data on age–height relationships of seedlings were obtained from United States Department of Agriculture, Bulletin 13, White Pine Under Forest Management. This relationship, existing in seedlings in planted pasture lands, was considered to approximate that which occurs in forested areas following fire.*

Qualitative studies of rot-producing fungi were made concurrently with quantitative examinations of felled trees. As the trees were dissected samples of decayed wood were obtained and slivers of wood from incipient rot areas were transplanted onto potato-dextrose agar in test tubes. Identification of most of the unknown decay organisms was made possible through these cultures.

Scaling Practices Employed in Field Studies

Board Feet

All sawlogs that would not cut one-third or more of their gross scale were culled. Sawlogs with less than four inches of sound wood around a center rot were culled. Other deductions were computed according to methods set forth in the *Manual of Scaling Instructions.*

Cubic Feet

In the development of cubic foot volumes for sawlogs a variety of methods of measurement were examined. As a basis for comparison, the actual cubic content of the logs was determined by a planimeter method*.

Cubic volume tables were used according to the following system:

1. Measurement of gross volume

(*a*) Volumes corresponding to mid-diameter of all logs were obtained.

(*b*) Volumes corresponding to alternate large and small diameters were obtained. All logs from the first tree were measured at their small diameters; all those from the second tree were measured at their large diameters. Subsequent trees were similarly measured, alternating large and small diameter measurements.

2. Measurement of decay volumes

(*a*) Decay deductions were made on the basis of rot visible on both ends of the log. Where rot was continuous throughout the log the amount of deduction was according to the schedule of Appendix 6 in the *Manual of Scaling Instruction.* Where butt type rot occurred, one half of the deduction of this schedule was applied.

(*b*) Decay deductions were made on the basis of the diameters measured in 1 (*b*) above; and according to the schedule presented in Appendix 6.

(*c*) The amount of rot was computed on the basis of continuous rot considered as a cylinder (i.e. table values of Appendix 2) and butt rot considered as a cone with its height equal to one half of the log length.†

* *The United States Department of Agriculture Form 558A (SB239) was utilized. This form is divided by a logarithmic grid. The outline of the tree is drawn to scale on this form and cubic volumes are readily obtained by passing; a planimeter around the outline of the tree. Spot checks indicated a difference of 2% or less between volumes obtained by this method and those computed by Smalian's formula.*

Smalian's formula: $\text{Cubic volume} = \frac{1}{2}(B + b)\,h$ *when*

B = *area of base, sq. ft.*
b = *area of top, sq. ft.*
h = *height in feet*

† $\text{Volume of a cone} = \frac{Bh}{3}$ *where* B = *area of base, sq. ft.;* h = *height in feet.*

It is noted that in the deductions for defect (*Manual of scaling instructions*) any log which has more than one half of its volume defective is considered a cull. If not culled because of this volumetric deficiency, logs were culled if they possessed less than four inches of sound wood around a center rot.

Total cubic foot volumes were determined for the entire tree. These volumes were computed for merchantable trees and for all trees sampled. The planimeter method, described above, was applied in these cases.

Decay in Relation to Age

Percentage of Trees with Decay

The increase in the incidence of decay with increasing age is set forth in Table I. It is evident that decay is present in approximately one third of the trees at the age of 50 years. The percentage of decay increases in older age classes until almost all trees exhibit decay. Of the 1012 trees examined 51.7% contained some measure of decay.

TABLE I

Relation between age and incidence of decay in Ontario white pine

Age class	Average age	Number of trees	Trees with decay	
			Number	Percentage
51- 70	63	391	155 (107)*	39.6 (27.4)*
71- 90	77	259	116 (76)*	44.8 (29.3)*
91-110	97	6	3	50.0
111-130	124	29	14	48.3
131-150	142	85	56	65.9
151-170	159	120	82	68.3
171-190	179	96	73	76.0
191-210	198	24	22	91.7
211-230	214	2	2	100.0
Totals	—	1012	523 (435)*	51.7 (43.0)*

* *At Barrys Bay a considerable number of trees were fire-scarred as the result of a ground fire which ran through the area 30 years after the stand was established (1913). Revised figures excluding fire-scarred trees are shown in brackets.*

Losses Caused by Decay

(*a*) *Board Feet (Ontario Log Rule)*

Data on the average, gross merchantable volume, decay volume, and net merchantable volume are presented in Table II and Fig. 2.

In Fig. 2 the increase in gross volume and decay volume with age is depicted. It will be seen that at 60 years of age decay volume is small and represents approximately 4% of the gross volume of the trees. At 120 years of age, however, the decay volume has increased to approximately 30% of the gross

volume. The decay volume continues to increase sharply and at 200 years the average gross volume of the trees is reduced by 40% through decay. The net volume for the average tree in each age class is shown.

TABLE II

AVERAGE GROSS VOLUME AND DECAY VOLUME FOR ONTARIO WHITE PINE ARRANGED ACCORDING TO AGE CLASSES

(Merchantable trees—Ontario Log Rule)

Age class	Number of trees	Average age	Average gross volume (bd. ft.)	Average decay volume (bd. ft.)
201-220	8	209	446	265
181-200	53	189	402	131
161-180	107	171	324	115
141-160	99	152	258	93
121-140	28	135	221	82
101-120	2	103	115	19
81-100	11	84	134	4
61- 80	74	71	103	14
41- 60	9	58	100	4
Totals	391	—	101,546	32,963

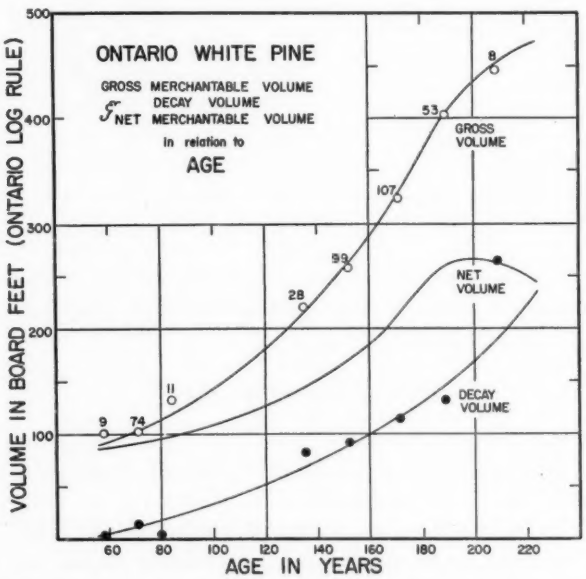


FIG. 2. Relation between age, gross merchantable volume, decay volume, and net merchantable volume for Ontario white pine (Ontario Log Rule).

TABLE III

COMPARISON OF THREE METHODS OF DETERMINING GROSS VOLUMES OF LOGS IN CUBIC FOOT MEASURE

Age class	Number of trees	Average age	Average gross volumes*		
			Method 1	Method 2	Method 3
201-220	8	209	79.0	79.4	74.4
181-200	53	189	71.3	73.7	70.1
161-180	107	171	56.9	56.0	55.9
141-160	99	152	46.1	46.0	45.0
121-140	28	135	38.9	40.1	38.6
101-120	2	103	21.1	23.9	23.0
81-100	11	84	26.2	25.4	26.3
61- 80	74	71	20.7	21.6	20.6
41- 60	9	58	22.0	21.4	21.0
Total	391				

**Gross volumes were determined as follows:*

Method 1: Logs were outlined by a planimeter for actual cubic content computations.

Method 2: Cubic content was derived from the alternate measurement of the large and small end diameters of the logs.

Method 3: Cubic content was derived from the measurement of median diameters of the logs.

NOTE: *Cubic foot tables were employed in Methods 2 and 3.*

TABLE IV

COMPARISON OF FOUR METHODS OF DETERMINING CUBIC VOLUMES OF DECAY IN LOGS

Age class	Number of trees	Average age	Decay volumes*			
			Method 1	Method 2	Method 3	Method 4
201-220	8	209	28.2	41.6	40.4	35.2
181-200	53	189	11.3	20.5	18.8	17.0
161-180	107	171	9.6	15.4	15.9	12.0
141-160	99	152	9.8	15.0	14.8	11.2
121-140	28	135	7.6	13.1	12.3	9.7
101-120	2	103	0.5	4.0	1.8	0.7
81-100	11	84	0.2	0.3	0.4	0.1
61- 80	74	71	0.8	1.8	1.9	1.3
41- 60	9	58	0.3	0.4	0.5	0.2
Total	391					

** Decay volumes were determined thus:*

Method 1: The actual cubic volume of decay was computed from planimeter readings.

Method 2: Measurement of decay was made at one end of the log only. The deduction for decay was read from Appendix 6 of the Manual of Scaling Instructions (Method 2, Table III).

Method 3: Measurement of decay at both ends of the log and deductions of one half the values presented in Appendix 6.

Method 4: "Trunk" rot considered as a cylinder, and so computed; "butt" rot considered as a cone with height equal to one half the log length and so computed. Both ends of each log examined.

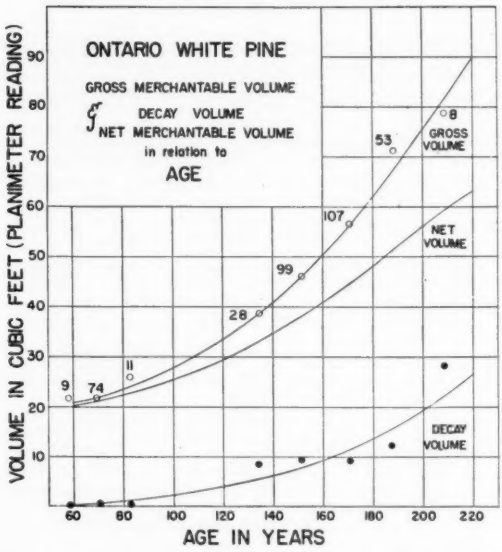


FIG. 3. Average gross volume, decay volume, and net volume for Ontario white pine; data arranged according to age-classes (merchantable trees, cubic foot measure—planimeter values).

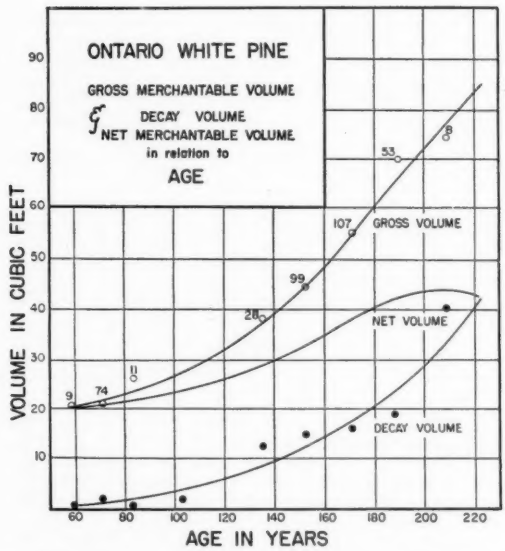


FIG. 4. Average gross volume, decay volume, and net volume for Ontario white pine; data arranged according to age classes (merchantable trees, cubic foot measure, manufacturing allowances).

(*b*) *Cubic Feet* (*Merchantable Logs*)

(*i*) *Measurement of Gross Volumes*

In order to assess their relative merits, a number of computation methods were used for the determination of gross volumes and decay volumes in cubic measure. Table III compares three methods of computing gross volume, and four methods of computing decay volume appear in Table IV.

(*ii*) *Measurement of Decay Volumes*

Fig. 3 was constructed from the data contained in Tables III and IV. This figure presents, in graphic form, the relationship between gross volume, decay volume, and age. In this array volumes were derived by the use of the planimeter and represent true values. No allowances were made for manufacturing losses.

Fig. 3 should be compared with Fig. 4 in which cubic foot volume tables have been used to determine gross and decay volumes. Gross volume was derived by Method 3 (Table III) and decay volume by Method 3 (Table IV). Thus, while Fig. 3 represents actual volumes of decay, Fig. 4 represents these volumes of decay with additional allowances for manufacturing waste.

(*c*) *Cubic Feet* (*Entire Tree Measurements*)

Table V and Fig. 5 set forth the complete tree volumes and the total volumes of contained decay. The values presented therein represent the entire volume of wood contained in the tree (excluding branches) above stump height, together with the amount of decay encountered in this volume. All trees on all plots are considered.

Pathological Rotation in Ontario White Pine

(*a*) *Board Feet* (*Ontario Log Rule*)

A comparison of gross and net periodic increments is presented in Table VI and Fig. 6.

It is evident in Table VI and Fig. 6 that the maximum net periodic increment occurs in trees from 170 to 180 years of age. Therefore, according to the Ontario Rule basis of measurement the pathological rotation for white pine occurs at this age.

It should be borne in mind, however, that data presented for trees in the older age classes are based on residual trees. These have escaped such agencies of mortality as disease, suppression, insects, and windthrow. It is possible that had trees which disappeared in the course of natural decimation been included, a slightly different gross increment would have resulted, and consequently a slightly different net increment would have been derived. This statement applies equally to the pathological rotation developed in Figs. 7 and 8 which follow.

TABLE V

AVERAGE GROSS VOLUMES AND DECAY VOLUMES FOR ONTARIO WHITE PINE ARRANGED ACCORDING TO AGE CLASSES

(All trees—entire cubic content)

Age class	Number of trees	Average age	Average gross volume (cu. ft.)	Average decay volume (cu. ft.)
201-220	8	209	86.5	28.6
181-200	53	189	82.9	12.2
161-180	110	171	64.3	9.4
141-160	120	152	48.3	8.5
121-140	57	133	32.1	5.6
101-120	10	115	13.9	1.0
81-100	51	84	17.1	0.6
61- 80	490	70	13.1	0.4
41- 60	113	57	10.7	0.3
Total	1012			

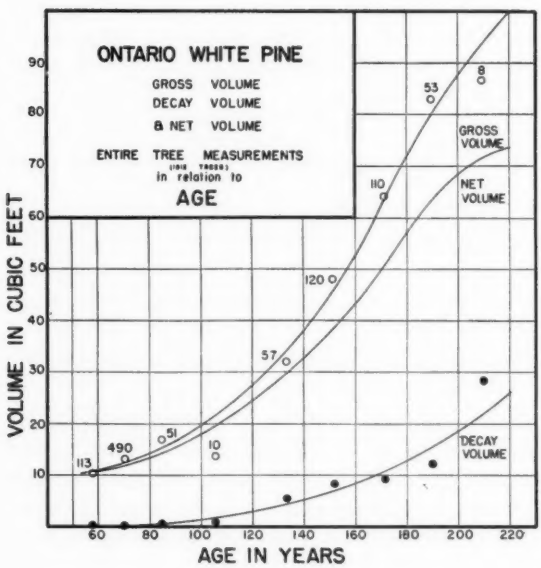


FIG. 5. Average gross volumes, decay volumes, and net volumes in relation to age for Ontario white pine.

TABLE VI

RELATION BETWEEN AGE, DECAY VOLUME, AND NET PERIODIC INCREMENT IN STANDS OF WHITE PINE

Basis—391 trees (curved values)

Age	Average gross merchantable volume (bd. ft.)	Average gross periodic increment (bd. ft.)	Average volume cull (bd. ft.)	Percentage of cull	Average net merchantable volume (bd. ft.)	Average net periodic increment (bd. ft.)
60	93	—	6	6.4	87	—
70	102	9	11	10.8	91	4
80	114	12	18	15.8	96	5
90	128	14	26	20.3	102	6
100	144	16	35	24.3	109	7
110	162	18	45	27.8	117	8
120	182	20	55	30.2	127	10
130	204	22	66	32.4	138	11
140	229	25	78	34.1	151	13
150	257	28	90	35.0	167	16
160	288	31	102	35.4	186	19
170	323	35	114	35.3	209	23
180	367	44	128	34.9	239	30
190	408	41	146	35.8	262	23
200	435	27	169	38.8	266	4
210	455	20	194	42.6	261	− 5
220	470	15	220	46.8	250	−11

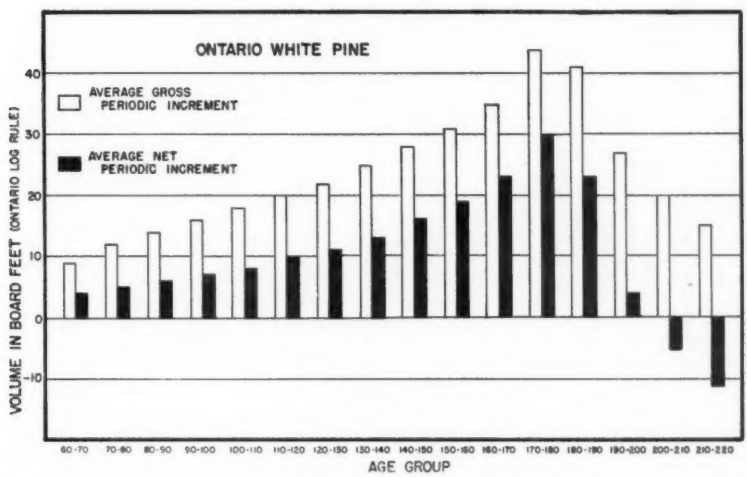


FIG. 6. Comparison of gross and net periodic increments in board feet for Ontario white pine of different age classes.

TABLE VII

RELATION BETWEEN AGE, DECAY VOLUME, AND NET PERIODIC INCREMENT IN WHITE PINE STANDS

Basis—391 trees (curved values)

Age	Average gross merchantable volume (cu. ft.)	Average gross periodic increment (cu. ft.)	Average decay volume (cu. ft.)	Percentage of decay	Average net merchantable volume (cu. ft.)	Average net periodic increment (cu. ft.)
60	21.0 (21.0)*	– (–)*	0.5 (0.5)*	2.4 (2.4)*	20.5 (20.5)*	– (–)*
70	21.8 (22.0)	0.8 (1.0)	1.0 (0.8)	4.6 (3.6)	20.8 (21.2)	0.3 (0.7)
80	23.0 (23.5)	1.2 (1.5)	1.6 (1.3)	7.0 (5.5)	21.4 (22.2)	0.6 (1.0)
90	25.0 (25.5)	2.0 (2.0)	2.8 (2.0)	11.2 (7.8)	22.2 (23.5)	0.8 (1.3)
100	27.0 (28.0)	2.0 (2.5)	3.8 (2.5)	14.1 (8.9)	23.2 (25.5)	1.0 (2.0)
110	29.3 (30.5)	2.3 (2.5)	4.9 (3.2)	16.7 (10.5)	24.4 (27.3)	1.2 (2.1)
120	32.0 (33.5)	2.7 (3.0)	6.1 (3.7)	19.1 (11.0)	25.9 (29.8)	1.5 (2.5)
130	35.6 (37.0)	3.6 (3.5)	7.9 (4.7)	22.2 (12.7)	27.7 (32.3)	1.8 (2.5)
140	39.4 (41.0)	3.8 (4.0)	9.6 (6.2)	24.4 (15.1)	29.8 (34.8)	2.1 (2.5)
150	43.8 (45.5)	4.4 (4.5)	11.6 (7.7)	26.5 (16.9)	32.2 (37.8)	2.4 (3.0)
160	48.8 (50.5)	5.0 (5.0)	13.9 (9.7)	28.5 (19.2)	34.9 (40.8)	2.7 (3.0)
170	54.5 (56.0)	5.7 (5.5)	16.8 (11.7)	30.1 (20.9)	37.7 (44.3)	2.8 (3.5)
180	60.2 (62.0)	5.7 (6.0)	20.2 (13.7)	33.6 (22.1)	40.0 (48.3)	2.3 (4.0)
190	66.0 (69.0)	5.8 (7.0)	24.1 (16.2)	36.5 (23.5)	41.9 (52.8)	1.9 (4.5)
200	72.0 (76.0)	6.0 (7.0)	28.6 (19.2)	39.7 (25.3)	43.4 (56.8)	1.5 (4.0)
210	77.5 (83.0)	5.5 (7.0)	34.2 (22.7)	44.1 (27.3)	43.3 (60.3)	−0.1 (3.5)
220	83.0 (90.0)	5.5 (7.0)	40.5 (26.7)	48.8 (29.7)	42.5 (63.3)	−0.8 (3.0)

* *Figures in brackets represent actual values based on planimeter measurements of volume, without allowance for manufacturing losses*

(*b*) *Cubic Feet*

Gross and net periodic increments are presented in Table VII.

Figs. 7 and 8 will serve to illustrate the indicated pathological rotation as based on cubic foot measurements.

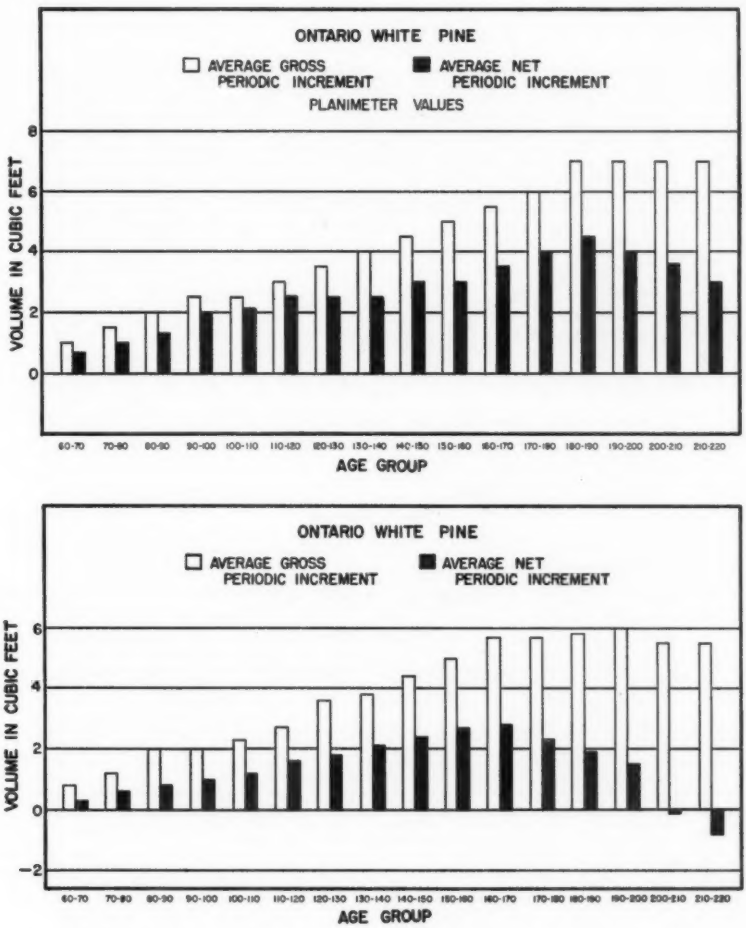


FIG. 7 (top). Comparison of gross and net periodic increments in cubic feet for Ontario white pine of different age classes (total cubic contents).

FIG. 8 (bottom). Comparison of gross and net periodic increments in cubic feet for Ontario white pine of different age classes (manufacturing losses deducted).

Cull Allowances Based on Age Groups

(*a*) *Board Feet* (*Ontario Log Rule*)

In Table VIII the gross yield per acre, total and percentage decay are set down for 10 1-acre plots. Actual merchantable volumes appear in this table. These data were used to construct a regression line (Fig. 9) depicting the percentage of decay in the various age classes. It is felt that the relationship

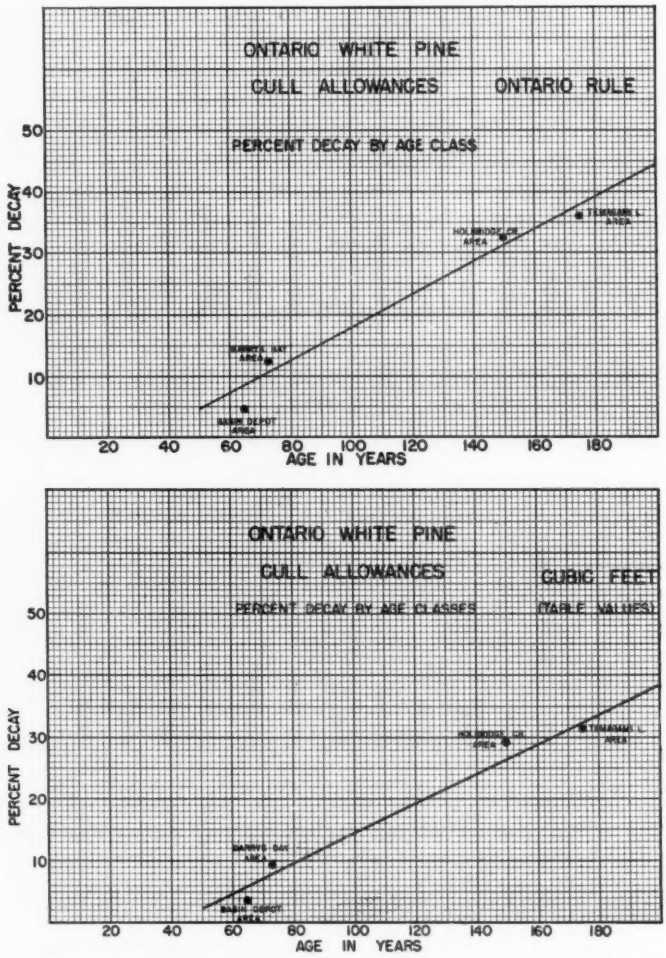


Fig. 9 (top.) Cull allowances according to age of stand—Ontario Log Rule.
Fig. 10 (bottom). Cull allowances according to age of stand—cubic foot measure.

TABLE VIII

GROSS VOLUME AND DECAY VOLUME IN 10 1-ACRE SAMPLE PLOTS—MERCHANTABLE TREES

(Board foot measure)

Area	Plot number	Volumes in ft. b.m.		Percentage decay	Number of trees per acre (merchantable)	Average age of trees
		Gross	Decay			
Basin Depot	1	1925	90	4.7	19	65
Barrys Bay	2	4295	529	12.3	39	71
	3	2101	280	13.3	23	75
	4	1897	256	13.5	15	80
Holdridge Cr.	5	17,317	5925	34.2	45	150
	6	16,563	5228	31.6	72	150
Timagami Lake	7	15,005	5919	39.4	59	168
	8	21,507	6759	31.4	56	176
	9	10,062	1989	19.8	30	178
	10	10,882	5988	55.0	33	187
Total					391	

as set forth in this graph may be of value in estimating cull allowances in cutting plans for even-aged white pine stands.

Actual decay relationships of the four sample areas have been superimposed on this chart to indicate its application. The probable cull allowances for any area may be obtained, provided the average age of the stand in question is known.

(*b*) *Cubic Feet*

Probable cull allowances based on cubic foot measurements with allowances for manufacturing waste have been computed from Table IX in a manner similar to that employed in board foot computations (*a*).

TABLE IX

GROSS VOLUME AND DECAY VOLUME IN MERCHANTABLE TREES

Basis—10 1-acre sample plots (cubic foot measure)

Area	Plot number	Volumes in cubic feet		Percentage of decay	Number of trees per acre (merchantable)	Average age of trees
		Gross	Decay			
Basin Depot	1	399.6	9.0	2.2	19	65
Barrys Bay	2	849.4	62.8	7.4	39	71
	3	408.9	38.8	9.5	23	75
	4	390.9	43.3	11.0	15	80
Holdridge Cr.	5	2998.7	945.1	31.5	45	150
	6	2834.3	757.0	26.7	72	150
Timagami Lake	7	2687.2	1006.2	37.4	59	168
	8	3668.8	991.9	27.0	56	176
	9	1795.5	225.6	12.6	30	178
	10	1884.0	903.6	48.0	33	187
Total					391	

Decay in Relation to Diameter

It is evident that in these even-aged white pine stands diameter is a poor criterion of decay. In any single area diameter may indicate tree vigor. Over a wide range of age classes, since age and diameter are correlated, it might be expected that decay would show a direct correlation with diameter. It will be seen, however, that although there is an increase in the volume of decay with increasing diameter, there is no uniform change in the relation this volume bears to the total volume within the diameter class. The average cull factor which appears in Fig. 9 is equally applicable to all diameters within any given age class.

Relationships between diameter class and average gross volume, decay volume, and percentage, are set forth in Tables X, XI, XII, XIII, and XIV and in Fig. 11.

TABLE X

RELATIONSHIP BETWEEN GROSS VOLUME AND DECAY VOLUME ACCORDING TO DIAMETER CLASSES

All areas—Ontario Log Rule

Diameter class midpoints	Number of trees	Average diameter	Average age	Average gross volume (b.f.m.)	Average decay volume (b.f.m.)	Percentage of decay
12.0	78	12.0	101	91.0	23.8	26.2
13.0	42	13.1	111	114.6	39.6	34.6
14.0	40	14.0	138	163.7	56.0	34.2
15.0	43	15.0	139	204.4	71.5	35.0
16.0	32	16.1	160	255.1	95.9	37.6
17.0	37	17.1	158	284.6	124.4	43.7
18.0	31	18.1	170	348.0	101.7	29.2
19.0	27	19.1	122	401.7	123.4	30.7
20.0	17	20.1	181	453.9	165.6	36.5
21.0	10	21.1	179	474.0	203.9	43.0
22.0	12	22.0	174	548.2	165.2	30.1
23.0	9	23.0	163	546.3	107.7	19.7
Over 23.5	13	26.4	170	770.9	166.8	21.6
Total	391					

TABLE XI

RELATION BETWEEN GROSS VOLUME AND DECAY VOLUME ACCORDING TO DIAMETER CLASSES

Basin Depot

Diameter class midpoints	Number of trees	Average diameter	Average age	Average gross volume (b.f.m.)	Average decay volume (b.f.m.)	Percentage of decay
12.0	10	12.1	64	90.2	5.3	5.9
13.0	7	13.0	63	105.1	5.3	5.0
14.0	1	14.5	68	150.0	—	—
15.0	1	15.2	72	137.0	—	—
Total	19					

TABLE XII

RELATION BETWEEN GROSS VOLUME AND DECAY VOLUME ACCORDING TO DIAMETER CLASSES

Barrys Bay

Diameter class midpoints	Number of trees	Average diameter	Average age	Average gross volume (b.f.m.)	Average decay volume (b.f.m.)	Percentage of decay
12.0	39	12.0	72	79.9	12.4	15.5
13.0	14	13.1	76	99.6	18.0	18.1
14.0	8	14.2	71	119.1	4.6	3.9
15.0	10	14.9	78	158.3	17.3	10.9
16.0	2	16.5	82	216.0	—	—
17.0	4	17.0	78	203.8	30.2	14.8
Total	77					

TABLE XIII

RELATION BETWEEN GROSS VOLUME AND DECAY VOLUME ACCORDING TO DIAMETER CLASSES

Holdridge Creek

Diameter class midpoints	Number of trees	Average diameter	Average age	Average gross volume (b.f.m.)	Average decay volume (b.f.m.)	Percentage of decay
12.0	16	12.0	148	100.4	46.2	46.1
13.0	11	13.1	144	131.9	63.5	48.2
14.0	16	14.1	152	181.5	76.9	42.4
15.0	13	14.9	138	224.6	71.2	31.7
16.0	8	16.2	141	267.8	67.8	25.3
17.0	11	17.1	151	287.4	156.7	54.5
18.0	11	18.1	152	327.2	46.4	14.2
19.0	9	19.1	154	390.8	123.1	31.5
20.0	2	20.1	144	387.0	278.0	71.8
21.0	2	21.2	145	338.5	62.5	18.5
22.0	5	22.0	157	507.2	135.4	26.7
23.0	5	23.1	143	496.8	49.2	9.9
Over 23.5	8	27.1	158	763.6	258.5	33.8
Total	117	—	—	—	—	—

TABLE XIV

RELATION BETWEEN GROSS VOLUME AND DECAY VOLUME ACCORDING TO DIAMETER CLASSES

Timagami Lake

Diameter class midpoints	Number of trees	Average diameter	Average age	Average gross volume (b.f.m.)	Average decay volume (b.f.m.)	Percentage of decay
12.0	13	12.2	160	113.2	44.8	39.6
13.0	10	13.1	157	123.1	67.5	54.8
14.0	15	14.1	164	169.5	64.7	38.2
15.0	19	15.1	175	218.4	103.9	47.6
16.0	22	16.0	174	254.0	114.8	45.2
17.0	22	17.0	177	298.0	125.3	42.0
18.0	20	18.2	181	359.4	132.1	36.8
19.0	18	19.1	180	407.1	123.6	30.3
20.0	15	20.0	185	462.8	150.6	32.5
21.0	8	21.0	187	507.9	239.2	47.1
22.0	7	22.0	186	577.6	186.6	32.3
23.0	4	23.0	187	608.2	180.8	29.7
Over 23.5	5	25.3	188	782.6	20.0	2.6
Total	178					

Decay in Relation to Rate of Growth

The relation between rate of growth, or vigor, and the amount of decay has been investigated for a number of tree species. Results of these investigations have not been consistent. In some cases it was determined that slow-growing trees exhibited greater volumes of decay than fast-growing trees; in other cases the opposite condition was held to apply; and in still other cases no well-defined differences in the amount of decay encountered in these two classes were observed.

To provide information about the relation between vigor and amount of decay in white pine the method outlined by McCallum (5) was employed. Trees in even-aged white pine stands were divided into two groups; a fast-growing (*a*) and a slow-growing group (*b*).

In group (*a*) were placed those trees whose gross cubic volume was greater than the curved value of average gross cubic volume presented for trees of their age in the age–volume curve (Fig. 12); and in group (*b*) were placed those trees whose gross cubic volume was less than the curved average gross cubic volume. Trees that fell on the average curve were rejected. Total cubic foot volume measurements for the entire tree were used in determining gross volume and decay volume.

It will be seen that slow-growing trees display more rot than fast-growing trees. Both the percentage of infected trees and the percentage of volume decayed are greater in the slow-growing trees. In all age classes which are represented in Table XV the gross cubic foot volume of fast-growing trees is substantially greater than for slow-growing trees. The average gross volume

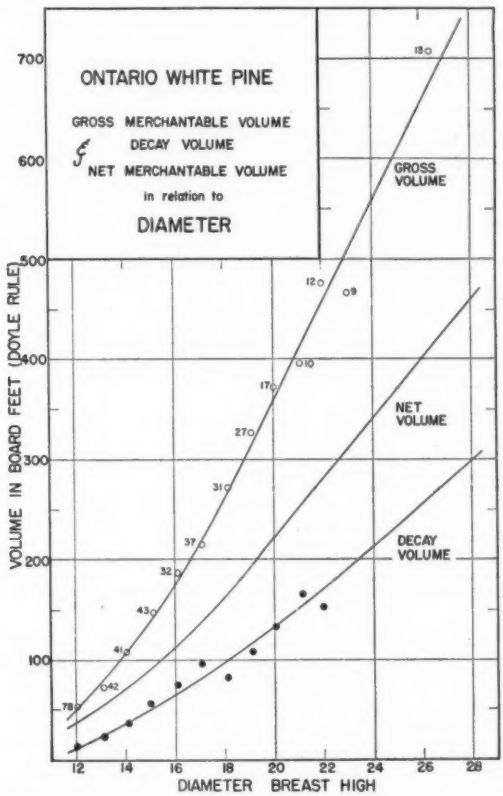


FIG. 11. Relation between the average gross merchantable volume, average decay volume, average net merchantable volume, and diameter at breast height.

for all fast-growing trees amounted to 79.5 cu. ft. For slow-growing trees this comparable volume was 38.7 cu. ft. The average volume of decay was greater for the fast-growing trees, but on a percentage basis the decay volume was much higher for slow-growing trees. This relationship is true for all the age classes represented. It will be seen further that in the younger age classes the percentage of infected trees is almost the same for both groups, but in older age classes the percentage infected increases among slow-growing trees.

Thus it would seem that, in these even-aged stands, trees which are best adapted to acquire materials for growth show lower relative decay losses. While approximately equal numbers of trees in each of the two groups were infected by rot-producing organisms, the amount of wood manufactured by fast-growing trees was much in excess of that manufactured by slow-growing trees.

TABLE XV

COMPARISON BETWEEN VOLUMES OF DECAY EXHIBITED BY FAST-GROWING AND SLOW-GROWING WHITE PINE TREES

(Merchantable trees only)

Age class	(*a*) Fast-growing trees						(*b*) Slow-growing trees					
	Number of trees	Trees with decay	Percentage with decay	Average gross volume (cu. ft.)	Average decay volume (cu. ft.)	Percentage of decay	Number of trees	Trees with decay	Percentage with decay	Average gross volume (cu. ft.)	Average decay volume (cu. ft.)	Percentage of decay
41- 60	4	1	25.0	31.4	0.6	1.9	5	—	—	22.8	—	—
61- 80	22	11	50.0	34.2	1.0	2.9	49	24	49.0	21.5	0.8	3.7
81-100	4	—	—	41.6	—	—	7	3	42.8	26.2	0.2	0.8
101-120	—	—	—	—	—	—	2	1	50.0	28.1	0.5	1.8
121-140	13	6	46.1	65.7	8.7	13.2	15	12	80.0	30.0	8.8	29.3
141-160	39	28	71.8	83.0	13.5	16.2	57	41	71.9	33.9	7.0	20.6
161-180	36	24	66.7	97.0	10.3	10.6	67	54	80.6	48.1	9.7	20.2
181-200	25	16	64.0	104.0	9.2	8.8	28	22	82.1	64.1	14.9	23.2
201-220	4	4	100.0	116.0	30.0	25.9	4	4	100.0	57.0	27.4	48.1
Total or average	147	90	*61.2*	79.5	9.4	*11.9*	234	161	*68.8*	38.7	7.5	*19.3*

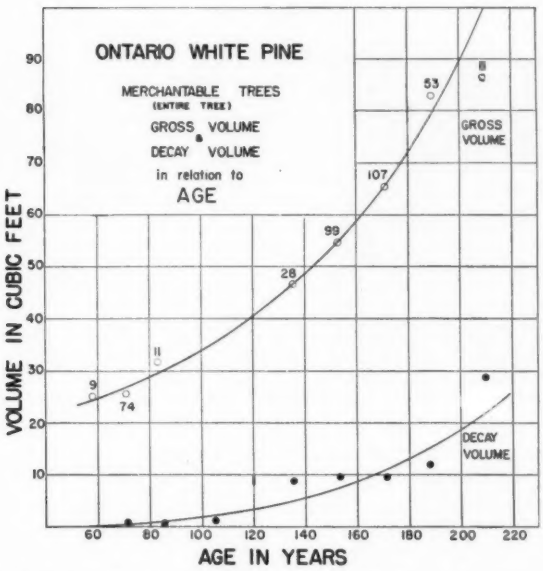


FIG. 12. Age-volume curve based on total tree volumes. Entire tree measurements, 391 trees.

One of the benefits accruing in a forest under management is a faster rate of growth for the final crop trees. Such an increased rate of growth (vigor) should result in increased net yields of utilized wood.

The Fungi That Cause Decay

PREVALENCE OF DIFFERENT TYPES OF DECAY

These studies have shown that, in white pine, trunk rots are responsible for more than 85% of the total loss through decay. On the basis of decay deductions in living trees, root and butt rots are of minor importance. The latter, however, are responsible for weakening at the base of the tree and may result in wind throw or breakage. The leaving of diseased trees as seed trees may be a dangerous practice since such trees are very prone to breakage under the excessive strains imposed by the opening up of stands.

A comparison between basal decays and trunk rots in respect to incidence and volume is presented in Table XVI. Since upward extension of infection is slow and examinations were carried out at stump height, it is probable that the actual number of trees with butt and root rot infections is slightly higher than recorded.

Observations indicate that advanced reproduction in older white pine stands may become infected through their root systems. Examination of 20 balsam fir seedlings of 2 in. d.b.h. chosen at random in sample plot 27

TABLE XVI

PREVALENCE OF DIFFERENT TYPES OF DECAY IN ONTARIO WHITE PINE

Type of decay	Total number of trees	Total volume of decay (cu. ft.)	Percentage of total volume (cu. ft.)	Total volume of decay (bd. ft.)	Percentage of total volume (bd. ft.)
Root and butt rots	108	619.3	12.4	4174	12.7
Trunk rots	199	4364.0	87.6	28,789	87.3
Totals	307	4983.3	100.0	32,963	100.0

(Timagami Lake area) revealed that roots and basal parts of *all* seedlings were badly decayed. Infection appeared to have occurred through root grafting with roots of infected trees or through wounded roots. Cultures of fungi from decayed wood established that this root and butt rot was caused by *Corticium galactinum* (Fr.) Burt. The evidence strongly suggests that this fungus may be responsible for a large mortality among advanced reproduction.

RELATIVE IMPORTANCE OF WOOD-DESTROYING FUNGI

Examination of Table XVII will reveal that of the 13 wood-rotting organisms recovered from living white pine trees, the white pocket rot fungus, *Fomes pini*, was the most important species encountered. This fungus causes both trunk rot and butt rot in Ontario white pine, but as a cause of trunk rot it is responsible for a greater loss in lumber. *F. pini* was responsible for 63% of trunk infections and 84% of the loss in board feet in this association was attributable to decay caused by this fungus. The loss in board feet (butts and trunks) as a result of decay caused by *F. pini* was 90% of the total loss through decay.

The majority of the fungi listed in Table XVII are well established as organisms causing decay in one or more coniferous species. Although quantitative studies had not been conducted previously, physiological and biological studies had been reported for many of the fungi causing decay in white pine.

FIG. 13. Fruiting body (conk) of *Fomes pini* produced at a branch whorl of a badly decayed tree.

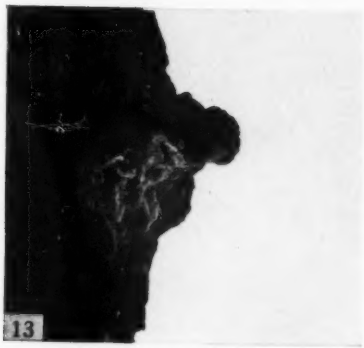
FIG. 14. White pocket rot caused by *F. pini* shown by a longitudinal section through the rotted portion of a white pine log. The white lenticular pockets are distinctive.

FIG. 15. Extensive pocket rot caused by *F. pini* in a white pine log. This log is a complete cull.

FIG. 16. White pine log cut across a whorl of branches to show a false conk (punk knot) developed in the region formerly occupied by a branch.

FIG. 17. Cross section of a white pine log showing an extensive area discolored by a "tomato-red" stain caused by the fungus *Corticium fuscostratum*. This stained area ultimately develops a powdery brown rot.

FIG. 18. Cross section of a white pine log showing the dark-brown cubical rot caused by *Merulius* sp.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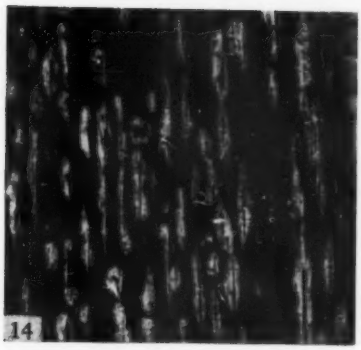
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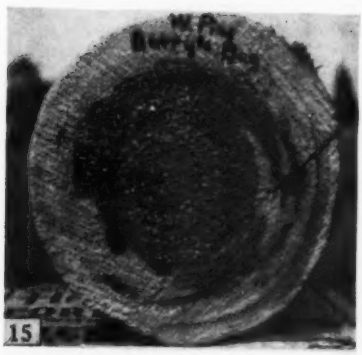
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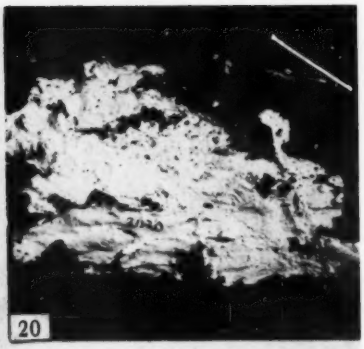
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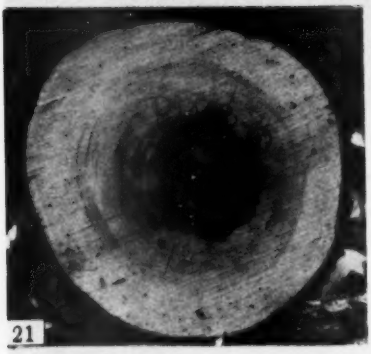
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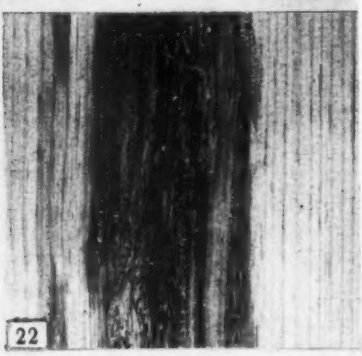
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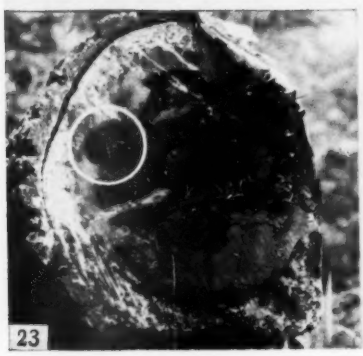
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This is particularly true of *Fomes pini* which occurs quite frequently in softwood forests. *Corticium galactinum*, on the other hand, has only recently come to be regarded as an important pathogen of forest trees (6). Although the loss among residual trees is small when compared to that caused by *F. pini*, *C. galactinum* was found to be the cause of more than 10% of all butt infections, and undoubtedly also causes considerable unrecorded mortality among mature trees and advanced reproduction.

External Indications of Decay

The points at which the fungi causing trunk rots entered the trees was difficult to determine definitely since any branch stub in a whorl might serve as a point of entry. This was especially true where the rot had become extensive. In such cases "blind knots" or "punk knots" were found at several whorls. "Punk knots" served as positive means of identification for rots caused by the white pocket rot fungus, *Fomes pini*. Swollen knots also occurred on such trees; when cut open these revealed the brown amorphous conklike tissue.

Other fungi associated with wood rots could not be determined with such ease. Since different fungi may produce similar rot patterns the best means of identification is the location of fruit bodies associated with the rot. Unfortunately, fruiting bodies do not develop readily on living pine trees, but may appear on stumps and cut ends of logs one or more years after cutting.

It was found necessary to rely upon cultures from samples of decay to obtain the identifications of the fungi listed in Table XVII. For the identification of many of these white pine decays the writer is indebted to Dr. Mildred K. Nobles, Division of Botany and Plant Pathology, Department of Agriculture, Ottawa. Many of the rots of white pine would be unrecorded had it not been for the cultural studies carried out by Dr. Nobles and her staff.

Discussion

This study was developed in order to provide those concerned with forest management in Ontario with information about the occurrence and volume of decay in white pine. It was considered advisable to sample immature, mature, and overmature stands. In some of the younger stands the majority

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FIGS. 19 and 20. Fruit bodies of *Corticium galactinum* developed on the root and bark of white pine.

FIG. 21. Butt log of white pine showing the center of the log completely destroyed by *C. galactinum*.

FIG. 22. Longitudinal section through a rotted log illustrating the stringy nature of the butt rot caused by *C. galactinum*.

FIG. 23. Fruit body (ringed) of *Polyporus schweinitzii* developing on a rejected butt-log two years after logging. The inconspicuous fruit body appears in the bracket form illustrated, but may also develop on an erect stalk growing from the roots of a badly rotted tree.

FIG. 24. Cross section of a white pine log showing the light brown cubical rot caused by *P. schweinitzii* at a height of 6 ft. above the ground. The rot disappeared at 8 ft. in this log.

TABLE XVII

THE FUNGI RESPONSIBLE FOR DECAYS OF WHITE PINE AND THEIR RELATIVE IMPORTANCE

Decay organism	Number of infections	Percentage of total number of infections	Cubic feet		Board feet	
			Volume of decay	Percentage of decay volume	Volume of decay	Percentage of decay volume
Trunk rots:						
Fomes pini (Thore) Lloyd	192	62.5	4264.6	85.6	27,773	84.3
Corticium fuscostratum Burt	4	1.3	73.5	1.5	596	1.8
Merulius sp.	1	0.3	6.1	0.1	302	0.9
Mixed and unknown	2	0.6	19.8	0.4	118	0.4
Butt and root rots:						
Fomes pini (Thore) Lloyd	29	9.4	188.1	3.8	2040	6.2
Corticium fuscostratum Burt	17	5.5	75.9	1.5	437	1.3
Corticium galactinum (Fr.) Burt	12	3.9	47.2	0.9	254	0.8
Polyporus schweinitzii Fr.	8	2.6	59.3	1.2	221	0.7
Merulius sp.	8	2.6	14.1	0.3	102	0.3
Omphalia campanella Fr.	7	2.3	70.1	1.4	279	0.8
Polyporus circinatus var. dualis Peck	4	1.3	54.2	1.1	370	1.1
Poria subacida (Peck) Sacc.	3	1.0	6.1	0.1	48	0.1
Poria asiatica (Pilât) Overh.	3	1.0	35.2	0.7	102	0.3
Coniophora puteana (Schum. ex. Fr.) Karst.	1	0.3	—	Trace	4	Trace
Mixed and unknown	16	5.2	69.1	1.4	317	1.0
Totals	307	99.8	4983.3	100.0	32,963	100.0

NOTE: *Three other fungi,* Polyporus balsameus *Peck,* Odontia bicolor (*Fr.*) *Bres., and* Peniophora gigantea (*Fr.*) *Massee, were identified as causal organisms of rot which occurred in trees that had not yet reached merchantable size. Of these* P. gigantea *which is associated with a pale brown sap rot, was isolated from samples of rot in fire-scarred trees.*

of the trees had not reached a merchantable size. Nevertheless, to permit identification of the fungi responsible for decay in various age groups and to prepare a complete picture of decay development, all trees were dissected.

Trees were segregated on the basis of merchantability. Merchantable trees (12 in. and over d.b.h. to an 8-in. top) were scaled in board feet and in cubic feet. The Ontario Log Rule was utilized to provide board foot measurements. The same logs were also scaled on a cubic foot basis. Several methods for computing cubic foot content and amount of cull were compared.

Certain age groups were not available for study, but their inclusion might be expected to make only minor changes in the average figures presented in the body of this report. These slight variations should not affect the application of the derived cull factors in compilation of forest inventories and forest management plans.

The results of this study have indicated that a well-defined relationship exists between age and decay. At 60 years of age the loss through decay is small, but it increases with increasing age. At 200 years of age the average gross board foot volume of the tree is reduced by 40%. When calculated on a cubic foot basis, the reduction in gross volume due to decay also reaches 40% at 200 years.

As computed upon returns in board feet (Ontario Log Rule), the pathological rotation for Ontario white pine as indicated by the period of maximum net periodic increment occurs in trees 170 to 180 years of age. On the basis of cubic content of logs (with allowances made for nonmanufacturable portions) the indicated pathological rotation is reduced by 10 years and occurs in the 160-to-170-year age group.

It is suggested that studies dealing with the incidence of rots subsequent to fires that leave basal fire scars could be carried out to advantage. Such scars present additional avenues for the entrance of decay fungi. It would be of interest to know whether fire-scarred trees develop greater amounts of rot than trees in which normal avenues for the entrance of fungi are dead branch stubs or bark-breaking injuries.

Acknowledgments

The writer wishes to express his indebtedness to Dr. J. E. Bier, Associate Chief, Division of Forest Biology, Ottawa, under whose supervision this study was carried out and whose aid in planning and conducting the field work was invaluable; and to Dr. J. H. Craigie, former Chief, Division of Botany and Plant Pathology, for permission to use the data for postgraduate studies.

Mr. T. W. Dwight, Professor of Forest Mensuration, Faculty of Forestry, University of Toronto, suggested methods in the analyses of quantitative data.

Grateful acknowledgment is made to the Ontario Department of Lands and Forests for providing a portion of the personnel and for assistance in transportation of the summer crews. The District Foresters and their associates, in whose administrative territories this study was conducted, were most helpful in supplying information and aid whenever assistance was requested.

Work undertaken on the limits of the Wm. Milne & Sons Lumber Co., Timagami; Gillies Bros. Ltd., Braeside; and Barrys Bay Lumber Co., Pembroke, received the interested support of company officials.

Dr. M. K. Nobles and her staff, of the Division of Botany and Plant Pathology, Ottawa, identified isolates from decays in white pine and made possible the inclusion of these records in this report.

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ISOLATION OF BACTERIOPHAGES FOR THE DETECTION AND IDENTIFICATION OF SOME SEED-BORNE PATHOGENIC BACTERIA[1]

By M. D. Sutton and H. Katznelson

Abstract

A strain-specific and polyvirulent phage for *Pseudomonas pisi* Sackett have been isolated from peas. The latter phage lyses also strains of *P. glycinea* Coerper, *P. lachrymans* (Smith and Bryan) Carsner, and *P. phaseolicola* (Burkholder) Dowson. The polyvirulent phage has been used successfully in detecting the presence of bacterial blight (*P. pisi*) in pea seed and plant tissue from infected fields. Specific phages for *P. atrofaciens* (McCullouch) Stevens and *P. coronafaciens* (Elliott) Stapp have been obtained, respectively, from wheat and oat seeds. Phages specific for *Xanthomonas translucens* f. sp. *hordei, secalis,* and *hordei-avenae* were isolated from barley and oat seed. Attempts to isolate viruses for *X. translucens* f. sp. *cerealis* and *undulosa* were not successful.

Introduction

Among plant pathologists there is a growing interest in the use of specific bacteriophages for the rapid identification of bacterial plant pathogens (6, 7, 8) because of the close relationships existing among the latter and because of the difficulty in distinguishing many of them by standard cultural procedures or serological techniques (2, 3). Members of the *Xanthomonas translucens* group, for example, are clearly distinguishable only on the basis of pathogenicity (1, 5) and, consequently, specific phages capable of differentiating the types represented in this or similar groups would be of great value. Pathogenic bacteria carried internally in seeds are particularly hard to isolate and identify, in consequence of which the phage technique may prove extremely useful, as was indicated in a previous paper (6).

During the last two years, an attempt has been made to isolate, from seed, phages for plant pathogenic pseudomonads commonly carried within seeds and for members of the *X. translucens* group. The results of these efforts are given in this paper.

Methods

For the isolation of phages for *Pseudomonas pisi*, pea samples from different sources were ground in nutrient broth (100 seeds in 500 ml.) in a Waring blendor for seven minutes. Each of the ground samples was divided in half. One-half of each sample was heavily inoculated with strain P11 and the other half with strain P26 of *P. pisi*. The samples were incubated overnight at room temperature. Suitable aliquots of the mixtures or of sterile Seitz filtrates of the mixtures were plated with a heavy suspension of these strains from 24 hr. yeast beef agar cultures. Plaques, where visible, were picked and placed in seeded broth, and serial passages were made daily to increase the titer of the phages.

[1] *Manuscript received November 17, 1952.*

Contribution No. 1217 from the Division of Botany and Plant Pathology and No. 351 from the Division of Bacteriology and Dairy Research, Science Service, Department of Agriculture, Ottawa, Canada.

This procedure was modified somewhat for cereal seed. Dry seed was ground and then divided into portions each of which contained the equivalent of 125–150 gm. of seed. Each portion received 150 ml. nutrient broth inoculated with a nutrient broth suspension of a particular organism from two 18-hr. yeast beef agar cultures, and was incubated overnight at room temperature with frequent stirring. The mixtures were filtered and the filtrates passed through sterile Seitz filters. The bacteriologically sterile filtrates were added in 1-ml. amounts to 10 ml. of broth in 50-ml. Erlenmeyer flasks seeded with the test organism. Clearing was observed after 5–10 hr. Clear cultures were filtered and serial passages made daily until the desired titer was obtained.

Diagnosis of internal infection of pea seed was carried out by means of the rapid phage plaque count technique described previously (6).

Results

Pseudomonas pisi—phage

Thirty-six samples of peas were tested. They yielded five phages: one was specific for strain P11 of *P. pisi* only and produced minute plaques, the other four lysed both P11 and P26 strains as well as the other species of phytopathogenic pseudomonads shown in Table I, and were probably identical. These four phages showed a wide range of activity. Thirty plaques were picked from one of these phages to determine whether or not it was pure or mixed. Each plaque yielded a phage capable of lysing the susceptible species (Table I), indicating that the phage was pure. (Fulton (4) has recently reported that phages lysing *P. tabaci* and *P. angulatum* also attacked *P. lachrymans*, *P. coronafaciens*, and *P. syringae*.) A close relationship between the susceptible species is indicated in the sixth edition of *Bergey's Manual of Determinative Bacteriology*.

The extreme specificity of the phage for strain P11 renders it largely useless for detecting *P. pisi* in pea seed. It might be considered also that the poly-

TABLE I

ACTIVITY OF PURE-LINE PHAGES FOR *Pseudomonas pisi* ON OTHER *Pseudomonas* SPECIES

Organism tested		Phage for *P. pisi* strain		Organism tested		Phage for *P. pisi* strain	
		P11	P26			P11	P26
P. angulata	(P7)	−	−	*P. phaseolicola*	(P3)	−	+
P. atrofaciens	(P8)	−	−	*P. phaseolicola*	(Pmp)	−	−
P. coronafaciens	(P9)	−	−	*P. pisi*	(P11)	+	+
P. coronafaciens	(P24)	−	−	*P. pisi*	(P26)	−	+
P. glycinea	(P10)	−	−	*P. syringae*	(P31)	—	—
P. glycinea	(P30)	−	+	*P. tabaci*	(P13)	−	−
P. lachrymans	(P28)	−	+				
P. aeruginosa	(499)	−	+	*P. fluorescens*	(629)	−	−

PLATE I

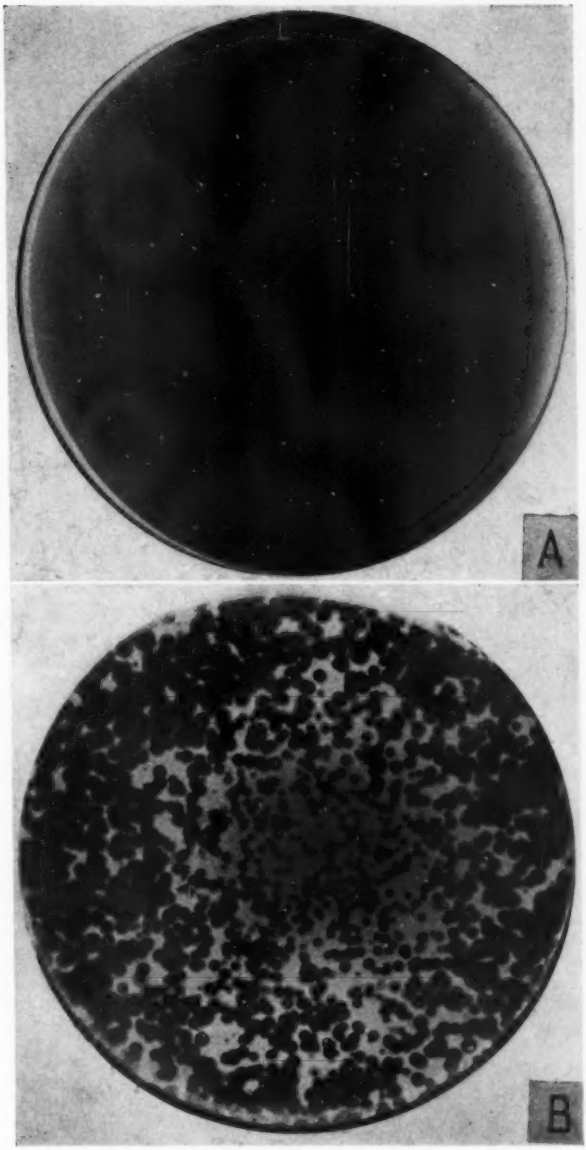

FIG. 1. Multiplication *P. pisi* phage in ground pea seed tissue.

A. Number of plaques (in 0.1 ml. sample) when phage initially added to sample of ground peas.
B. Number of plaques 6–12 hr. afterward.

virulence of the other four phages may also preclude their use for that purpose. Since it is unlikely, however, that some other bacterial pathogen would be found internally in pea seed, it would appear practicable to use these phages in the rapid phage plaque count technique (6) to detect this organism. In a preliminary trial with one of these phages, several lots of peas were tested by this technique. One lot (Pp 1) had been reported as being infected with bacterial blight to the extent of 16%. The presence of organisms susceptible to the polyvirulent phage in this lot was evident (Table II and Fig. 1). Isolates from this sample yielded a number of cultures which were lysed by this phage.

Seven other samples of peas from fields reported as infected with bacterial blight were obtained at a later date and tested with the same phage by the same technique. Each of the seven samples gave a positive result (a striking increase in the number of plaques after a suitable incubation period). *P. pisi* was readily isolated from several of the mascerated seed samples and produced typical lesions when reinoculated into pea plants.

Obviously, however, many more tests, supported by pathogenicity tests with isolates from the samples, are required before this method and this phage can be recommended for use in detecting internally-borne infection of *P. pisi* in pea seed, or for identifying the other susceptible species in suspected material.

TABLE II

INTERNAL INFECTION OF PEAS AND INFECTION ON PEA LEAVES WITH BACTERIAL BLIGHT AS DEMONSTRATED BY THE PHAGE PLAQUE COUNT TECHNIQUE

Pea lot	Hours	Plaque count in 0.1 ml.			
		Sample 1	Sample 2	Sample 3	Sample 4
Pp 1a	0	34	24	30	25
	6	270	15	17	12
	24	3000	10	12	6
Pp 1b	0	106	90	63	80
	6	45	5	23	Confluent
Pp 2	0	65	65	58	87
	6	1	2	7	22
Pp 3	0	74	87	104	90
	6	28	35	6	10

Pea leaves	Hours	Plaque count in			
		0.1 ml.	0.2 ml.	0.1 ml.	0.2 ml.
		Sample 1		Sample 2	
	0	13	32	82	156
	12	60	138	Confluent lysis	Confluent lysis

Another possible application of the rapid phage plaque count technique was suggested recently when two samples of pea plants were brought in from the field. The leaves were spotted with lesions which appeared to be caused by the bacterial blight organism (*P. pisi*). This diagnosis was corroborated by placing badly spotted areas of leaves in nutrient broth and adding a known number of particles of the polyvirulent phage. Plaque counts were made at once, and after 12 hr. As may be noted in Table II, there was a fourfold increase in number of plaques in one sample and a very great increase in the other. It would appear, therefore, that this method might be applied successfully to a rapid laboratory diagnosis of infected plant material, not only for *P. pisi*, but, if homologous phages were available, for other bacterial diseases of plants as well.

P. atrofaciens—phage

Of 60 samples of wheat collected in different parts of Canada, 59 yielded a phage specific for an avirulent strain (P8) of this organism (originally strain PA 13 of Dr. W. H. Burkholder of Cornell University). None of these phages was active on any of the other pseudomonads listed in Table I. Furthermore, none lysed three new pathogenic strains of *P. atrofaciens* supplied by Dr. W. A. F. Hagborg, of the Dominion Laboratory of Plant Pathology, Winnipeg, Man. The very high degree of specificity of this phage for the avirulent strain makes the wide distribution of the phage somewhat of a puzzle. Further work is needed to elucidate the implications of these observations.

P. coronafaciens—phage

Forty-eight samples of oat seed were divided into eight lots of six samples each and each lot was tested for the presence of phages. Two lots yielded a phage active against two strains of *P. coronafaciens* (P9 and P24), but not lytic on any of the other *Pseudomonas* species listed in Table I.

X. translucens—phages

Twenty-four samples of barley seed were divided into four lots, each lot comprising six samples. The six samples of each lot were pooled, ground, and

TABLE III

SPECIFICITY OF *Xanthomonas translucens* PHAGES

Organism		Phage for		
		f. sp. *hordei*	f. sp. *secalis*	f. sp. *hordei-avenae*
X. translucens f. sp. *hordei* (P36)		+	−	−
" " f. sp. *secalis* (P38)		−	+	−
" " f. sp. *hordei-avenae* (P50)		−	−	+
" " f. sp. *undulosa* (P34)		−	−	−
" " f. sp. *cerealis* (P37)		−	−	−
" " f. sp. " (P25)		−	−	−
X. phleipratensis (P35)		−	−	−

inoculated with fresh young cultures of *X. translucens* f. sp. *hordei*, *hordei-avenae*, *secalis*, and *cerealis*. Specific phages for the formae speciales *hordei* and *secalis* of the *X. translucens* group were isolated.

Forty-eight samples of oats were similarly divided into eight lots, ground, and inoculated with cultures of *X. translucens* f. sp. *cerealis* and *hordei-avenae*. Two lots yielded a specific phage for *hordei-avenae*. No phage was isolated for *X. translucens* f. sp. *undulosa* or *cerealis* from 90 samples of wheat or 12 samples of rye inoculated with these organisms.

The phages which were isolated were highly specific for their bacterial hosts, as indicated in Table III, but were not active on any of the other species of *Xanthomonas* listed in Table II of a previous paper (6).

Discussion

The isolation of the phages described above makes possible their utilization in the diagnosis and identification of their seed-borne bacterial hosts, as in the case of halo blight of beans (6). The unusually wide distribution of the strain-specific phage for *P. atrofaciens* is difficult to interpret at present.

Of particular interest is the discovery of phages for three of the five form-species of *X. translucens* (5). The specificity of these phages may be of considerable value in the rapid laboratory identification of these organisms. Boosalis (1) has recently described a vacuum technique which permits detection of these organisms within five days, the method being based on the appearance of disease symptoms on seedlings. A diagnostic procedure which may be carried out in 24 hr. to 48 hr. in the laboratory would be of distinct advantage. The use of phage for this purpose is a promising recent development (6).

Acknowledgment

The authors are indebted to all those who have kindly supplied seed samples during the course of this work and to Mr. W. Bell for technical assistance.

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NITROGEN AND VITAMIN REQUIREMENTS OF *PSEUDOMONAS HYDROPHILA*[1]

By Florence R. Tamboline

Abstract

Yeast extract and vitamin-free casamino acids were found to be equivalent as sources of nitrogen for the growth of *Pseudomonas hydrophila* in a glucose – mineral salts medium. The addition of a mixture of thiamine, riboflavin, pantothenic acid, pyridoxine, nicotinic acid, para-aminobenzoic acid, biotin, and folic acid to the medium containing vitamin-free casamino acids did not stimulate growth. About 67% as much growth was obtained with a mixture of 20 amino acids and asparagine as with the vitamin-free casamino acids and the mixture could be replaced by any one of asparagine, aspartic acid, serine, and alanine. Of the 11 simple nitrogen compounds tested, including urea, nitrates, and ammonium salts, only ammonium citrate and dibasic ammonium phosphate were utilized appreciably. A simple synthetic medium consisting of ammonium citrate, glucose, and mineral salts was found to give approximately the same amount of growth as the more complex yeast extract – glucose – mineral salts medium.

Introduction

Although *Pseudomonas hydrophila* has been used extensively in fermentation studies (8, 9, 10), little quantitative information is available on its nutritional requirements. Yeast extract has been used as the source of nitrogen and vitamins in the basal medium commonly employed in these laboratories for studies of the fermentation of purified substrates. In the present investigation an attempt has been made to replace the yeast extract with chemically defined sources of nitrogen and vitamins.

Materials and Methods

The organism employed in this work was *P. hydrophila* N.R.C. 492. Stock cultures were maintained on 1.0% glucose–0.5% yeast extract agar slants, and inocula were prepared from 24-hr. cultures on this medium by transferring one 3 mm. loopful of cells to 10 ml. of sterile 0.9% sodium chloride solution. One drop of this suspension was used to inoculate each tube of test medium. The cultures were incubated at 30° C. and turbidity was measured after 24, 48, and 96 hr. using an Evelyn photoelectric colorimeter with a 660 mμ filter. All determinations were made on duplicate cultures. In some experiments the pH of each culture was also determined. The most promising media were retested from one to five times, and the optical density values given in the tables are the average values from all the trials made with each medium. Although small variations were observed in the optical density values on replication, the relative growth levels were unchanged.

The methods employed were those commonly used for vitamin and amino acid assays. All glassware was cleaned with hot concentrated sulphuric acid

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and was then rinsed thoroughly with distilled water. The pH of each test medium was adjusted to 6.8 with sodium hydroxide and the medium dispensed in 10-ml. quantities in 15 × 150 mm. test tubes. Media containing urea and ammonium salts were sterilized by filtration using sintered glass filters; media containing added vitamins were sterilized by autoclaving for 10 min. at 121° C.; all other media were autoclaved for 15 min. at 121° C.

The test media, made up with distilled water, consisted of glucose, 1.0%; potassium dihydrogen phosphate, 0.05%; dipotassium hydrogen phosphate, 0.05%; magnesium sulphate heptahydrate, 0.02%; ferrous sulphate heptahydrate, 0.001%; manganese sulphate tetrahydrate, 0.001%; sodium chloride, 0.001%; various nitrogen sources in concentrations to supply a total of 0.076% nitrogen. When two or more amino acids were employed in the same medium, they were used in the same proportion in which they occur in casein (4). Since Gordon *et al.* (4) did not record the presence of hydroxyproline, cysteine, and asparagine in casein, hydroxyproline was added in the same relative concentration as cystine (12), cysteine in the same relative concentration as isoleucine (6), and asparagine in the same relative concentration as glutamic acid (6). When DL amino acids were used, they were added in twice the calculated amounts.

Vitamin requirements were determined in a basal medium consisting of glucose, mineral salts, and vitamin-free casamino acids, using eight growth factors in the following concentrations per 100 ml. of medium: thiamine hydrochloride, 20 μgm.; riboflavin, 40 μgm.; calcium pantothenate, 20 μgm.; pyridoxine hydrochloride, 40 μgm.; para-aminobenzoic acid, 20 μgm.; nicotinic acid, 20 μgm.; biotin, 0.08 μgm.; folic acid, 0.05 μgm. (2, pp. 155, 157).

Results and Discussion

Vitamin Requirements

P. hydrophila was found to grow as well on vitamin-free casamino acids, Difco, as on yeast extract*, Difco, or on casamino acids which had not been freed of vitamins (Casamino Acids Technical, Difco). The addition of a mixture of the eight growth factors to the vitamin-free casamino acids medium did not stimulate growth.

Since vitamin-free casamino acids appeared to be as satisfactory a nitrogen source as yeast extract, and since its constitution is more nearly defined than that of yeast extract, it was used as a reference in the studies on nitrogen requirements.

* *The nitrogen content of each medium (0.076%) was calculated to supply approximately the same amount of nitrogen as 0.5% yeast extract on the basis of 11% nitrogen in Difco yeast extract (Difco Laboratories analysis) and 7% nitrogen in Difco vitamin-free casamino acids (2). However, the vitamin-free casamino acids medium always gave about 30% better growth than the yeast extract medium. The samples of yeast extract and vitamin-free casamino acids used in the experiments were therefore analyzed for nitrogen and were found to contain 8.5% and 7.9% nitrogen respectively. When media (containing 0.076% nitrogen) were prepared using the two materials in concentrations according to the corrected values, the same amount of growth was obtained on each medium.*

Amino Acid Requirements

After establishing that *P. hydrophila* could synthesize all of the vitamins necessary for growth, a survey was made of the organism's amino acid requirements (Table I). An average of about 67% as much growth was obtained with a mixture of 20 amino acids and asparagine as with the vitamin-free casamino acids. When each of the amino acids and asparagine was omitted in turn from the complete mixture, growth was reduced appreciably only in the absence of asparagine, serine, histidine, or tyrosine. But when each of the four was tested as the sole source of nitrogen, approximately the same amount of growth was obtained with asparagine (by 48 hr.) and serine (by 96 hr.) as with the complete mixture, whereas very poor growth was obtained with histidine and tyrosine. Alanine and aspartic acid, which are closely related chemically to serine and asparagine, respectively, also supported good growth. From these results it appears that any one of several amino acids is a satisfactory nitrogen source for *P. hydrophila*.

The response to aspartic acid differed considerably from that to asparagine, the amide of aspartic acid. The growth curve for the asparagine cultures followed the general pattern of the curves for cultures on vitamin-free casamino acids and on the amino acid mixture, with a cessation of growth after about 48 hr. incubation. The aspartic acid cultures had a similar growth rate but, unlike the asparagine cultures, growth continued at the same rate for the entire 96-hr. incubation period. The total amount of growth obtained with aspartic acid was thus significantly greater than that obtained with asparagine. Furthermore, in the interval between the 48- and 96-hr. readings there was a decided shift in the pH of the aspartic acid cultures towards alkalinity. It is possible that the amide group of asparagine may be less readily utilized than

TABLE I

AMINO ACID REQUIREMENTS OF *Pseudomonas hydrophila* N.R.C. 492

Nitrogen source† (0.076% N_2)	Optical density* × 100			Final pH	
	Period of incubation, hr.				
	24	48	96	48	96
Vitamin-free casamino acids	46	64	61	6.15	6.65
20 amino acids + asparagine	29	42	45	—	—
L(−)asparagine . H_2O	24	40	40	5.15	5.20
DL-aspartic acid	20	35	68	5.60	7.30
DL-serine	6	35	49	6.30	6.95
DL-alanine	2	11	43	5.70	6.15
L(+)histidine . HCl	3	6	8	—	—
L(−)tyrosine	3	4	3	—	—

† *Basal medium contained 1.0% glucose and mineral salts (0.05% KH_2PO_4, 0.05% K_2HPO_4, 0.02% $MgSO_4 . 7H_2O$, 0.001% $FeSO_4 . 7H_2O$, 0.001% $MnSO_4 . 4H_2O$, and 0.001% NaCl).*

* *Average values from several experiments. See text.*

the amino group, a suggestion already made by Anderson (1). The fact that there would be twice as many amino groups available in the aspartic acid medium than in the asparagine medium might then account for superior growth on the former.

During the first 24 hr. of incubation practically no growth was obtained with either serine or alanine. At 96 hr., however, growth was equivalent to that obtained with asparagine and the amino acid mixture. Using several combinations of serine and asparagine as nitrogen sources, it was found that when three-quarters of the nitrogen was supplied by serine the growth curve was almost identical with that for serine alone, and, when only one half or less of the nitrogen was supplied by serine, the growth curve followed the same pattern as with asparagine alone. Woolley and Hutchings (12) also observed a long lag period with *Streptococcus zymogenes* when it was grown on certain amino acid combinations. These findings emphasize the importance of the length of the incubation period in the evaluation of the ability of an organism to utilize various substances.

Utilization of Simple Nitrogen Compounds

The utilization by *P. hydrophila* of urea, nitrates, and the ammonium salts of both organic and inorganic acids is shown in Table II, with the various compounds arranged in decreasing order of efficiency. Of the 11 compounds tested, ammonium citrate gave the best growth with values essentially the same as those obtained with the complete amino acid mixture (Table I). Dibasic ammonium phosphate was a reasonably satisfactory source of nitrogen

TABLE II

UTILIZATION OF SIMPLE NITROGEN COMPOUNDS BY *Pseudomonas hydrophila* N.R.C. 492

Nitrogen source† (0.076% N_2)	Optical density* × 100			Final pH	
	Period of incubation, hr				
	24	48	96	48	96
Vitamin-free casamino acids	46	64	61	6.15	6.65
Ammonium citrate	33	46	47	5.75	5.85
$(NH_4)_2HPO_4$	32	28	27	5.95	6.25
$NH_4H_2PO_4$	23	20	15	5.35	5.40
$(NH_4)_2SO_4$	16	18	18	4.75	4.50
Ammonium succinate	14	14	14	5.50	5.60
Ammonium acetate	8	14	17	6.55	6.65
Urea	14	12	15	6.35	6.65
NH_4Cl	11	11	11	4.90	5.15
NH_4NO_3	7	6	3	5.65	5.65
$NaNO_3$	4	6	3	5.75	5.70
KNO_3	4	4	2	5.65	5.70

† *See Table I for basal medium.*
* *Average values from several experiments. See text.*

but supported an average of only about 70% as much growth as did ammonium citrate. Very poor growth was obtained with the nitrates. The other compounds tested were utilized only to a limited extent.

The variability in growth response to the several ammonium compounds tested demonstrates that these salts are not equally utilized by *P. hydrophila*. Most reports on the nutrition of bacteria state merely that an organism can or can not utilize ammonia as a source of nitrogen, but seem to have attached little significance to the particular ammonium salt used. Ammonium chloride and ammonium sulphate are usually employed in media for general use and ammonium phosphate is frequently used to grow cells for metabolic studies. To the author's knowledge no quantitative survey has ever been made of the relative merits of ammonium salts as sources of nitrogen for specific bacteria. The statement that an organism is unable to utilize ammonia nitrogen is frequently based on the results of experiments with a limited number of ammonium salts. It is apparent from Table II that any study restricted to a few ammonium compounds might easily lead to erroneous conclusions.

Of the substances tested as possible sources of nitrogen for *P. hydrophila*, ammonium citrate is the most promising for use in a synthetic medium. Table III shows that doubling the nitrogen content over that used for the rest of the study (1.2% ammonium citrate) resulted in approximately 17% better growth in 24 hr. than that obtained with the best of the other chemically defined nitrogen sources, and about the same amount of growth in 96 hr. as that obtained with vitamin-free casamino acids.

The growth of *P. hydrophila* on ammonium citrate in the absence of glucose (Table III) indicates that this organism can utilize ammonium citrate as a

TABLE III

RESPONSE OF *Pseudomonas hydrophila* N.R.C. 492 TO DIFFERENT CONCENTRATIONS OF AMMONIUM CITRATE AND GLUCOSE†

Ammonium citrate, %	Glucose, %	Optical density* × 100		
		Period of incubation, hr.		
		24	48	96
0.6	0.0	15	25	19
0.6	1.0	33	46	47
0.6	2.0	35	52	53
0.6	4.0	31	34	28
1.2	1.0	41	54	58
1.2	4.0	37	48	59
Vitamin-free casamino acids (1.0% glucose)		46	64	61

† *See Table I for mineral salts in medium.*
* *Average values from several experiments. See text.*

source of carbon and energy as well as of nitrogen. As might be expected on the basis of the low carbon content of the glucose-free medium, growth was much reduced over that obtained when glucose was available.

The fact that ammonium citrate gave the best growth of all the simple nitrogen compounds studied is rather surprising in the light of the general observation that bacterial cell membranes are less permeable to the citrate ion than to the other anions tested (7, 11). It is possible that the citrate ion may have stimulated the energy-producing mechanism of the organism, perhaps in a manner analogous to the stimulation obtained by Johnson and Cohn (5) when they added malic acid to a "complete" medium for *Escherichia coli*. In a somewhat similar fashion Evans and Niven (3) found that the addition of sodium citrate to a medium adequate for the growth of certain lactobacilli almost tripled the amount of growth obtained in 48 hr.

Ammonium citrate in 1.2% concentration was equivalent to yeast extract as a source of nitrogen for the growth of *P. hydrophila*. It would be of interest to determine whether ammonium citrate would be equally suitable as a source of nitrogen for fermentation. Furthermore, an investigation of the specific role of the citrate ion in the metabolism of this organism might explain its unexpected response to ammonium citrate.

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FOREST COMMUNITIES IN NORTHWESTERN ALBERTA[1]

By E. H. Moss[2]

Abstract

Spruce, tamarack (larch), balsam fir, pine, and poplar communities of the region are described in terms of floristic composition and ecological relationships. The white spruce (*Picea glauca*) association is regarded as the climax type of the region. Of four phases or faciations presented by the white spruce association, the feather moss faciation appears to be the climax to which the other faciations tend to develop. Two black spruce (*Picea mariana*) communities are recognized, the black spruce – feather moss association and the black spruce–peat moss association. Of these, the former is characterized by "feather mosses" such as *Hylocomium splendens* and has developed on relatively level terrain without much peat formation, whereas the latter has a *Sphagnum* floor and has arisen in definite depressions through acid bog stages with the production of considerable peat. The black spruce – bog moss community is interpreted as subclimax, with natural succession to the black spruce – feather moss association. The tamarack (*Larix laricina*) community has many features in common with the black spruce – peat moss association but differs markedly, not only in its dominant species, but because of its development from a *Drepanocladus–Carex–Betula* bog under persisting wet conditions. Succession to black spruce commonly occurs. Balsam fir (*Abies balsamea*) is relatively rare in the region and usually grows in mixed stands with white spruce, paper birch, aspen, and balsam poplar. Two divisions of the pine association are recognized, the jack pine (*Pinus banksiana*) and the lodgepole pine (*P. contorta* var. *latifolia*) consociations. For each of these, two phases are described, the pine – feather moss faciation on the more shaded sites and the pine–heath faciation on the more open and drier areas. Knowledge of the ranges of these two pines in northern Alberta and concerning hybrids between the species is extended. The poplar association, classified as aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) consociations, is considered in relation to other vegetation, especially prairie grassland and white spruce. Encroachment of aspen poplar upon native grassland is counteracted by various factors, notably burning. Natural succession of poplar and pine to white spruce is impeded chiefly by forest fires. Some attention is given to phytogeographical problems of this transition region.

Introduction

The region of this investigation is part of the broad transition belt between the Northern (Boreal) and Cordilleran forests. It may also be regarded as transitional between the northern forest zone and the prairie. Little has been published on the plant communities of the region, apart from a recent paper (12) on the grassland vegetation. Extensive botanical studies have been carried out by Raup (14, 15, 16, 17) to the north, east, and west of the region and by others (5, 8, 9, 13) in central Alberta to the southeast. The present paper aims therefore to describe the floristic composition and ecological relationships of the chief forest types of this interesting and relatively unknown region. In addition to the large area of northwestern Alberta, a small portion of British Columbia has been brought within the scope of the investigation (Fig. 1). For a general account of the region an earlier paper by the writer (12) may be consulted.

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The most common of the forest tree species of the region are the aspen or white poplar (*Populus tremuloides*), the balsam or black poplar (*P. balsamifera*), the white spruce (*Picea glauca*), the black spruce (*P. mariana*), the jack pine (*Pinus banksiana*), and the lodgepole pine (*P. contorta* var. *latifolia*). Less prominent are the tamarack (*Larix laricina*), the balsam fir (*Abies balsamea*),

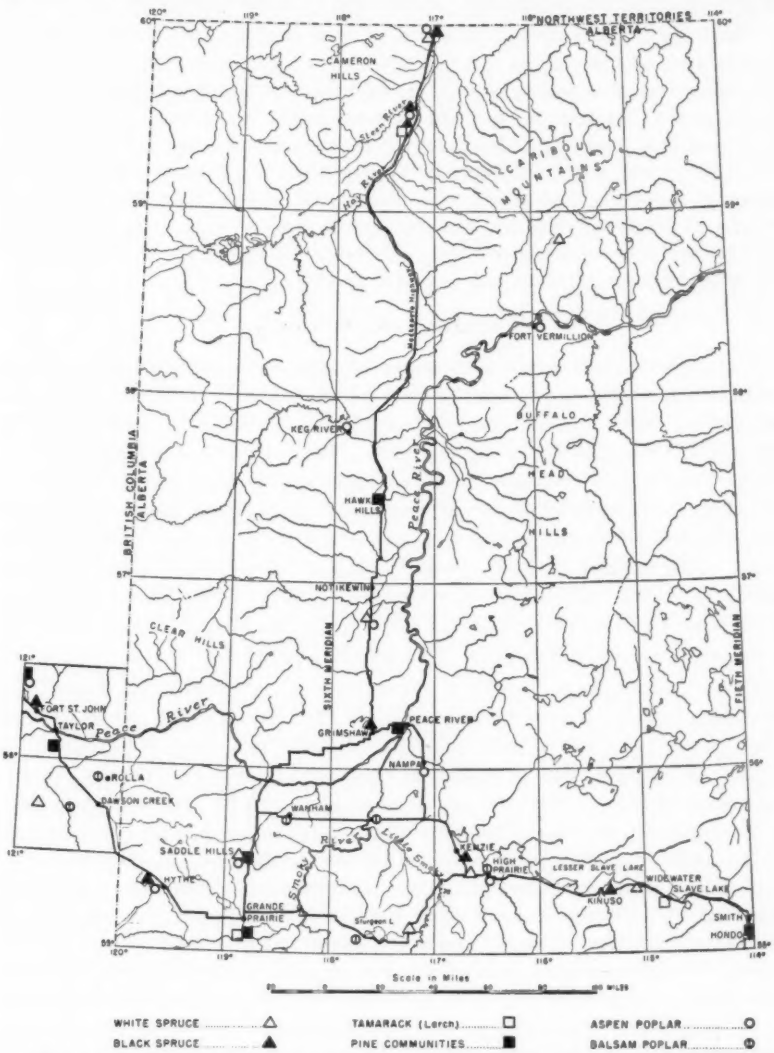

FIG. 1. Map of northwestern Alberta and a small portion of British Columbia, showing the location of forest stands to which special study was given.

and the white or paper birch (*Betula papyrifera*). These species occur in various kinds of mixed woods, as well as in pure or nearly pure stands. Actually, a very large proportion of the forest is mixed, aspen poplar and white spruce predominating. Despite the diversity of mixed stands, certain forest types or communities are recognizable as entities that tend to develop, to persist, and often to reappear (successionally) when destroyed.

The forests are described in terms of such well known concepts as the association and the climax, concepts that have come in for some criticism by several ecologists in recent years. Despite this criticism (with some of which the present writer agrees), these concepts are held to be of great value, at least in describing, classifying, and trying to understand vegetation. Though associations and other subjectively determined categories are featured, the paper is especially concerned with the actual species of particular forest stands, their abundance and disposition, as well as with major ecological changes and their apparent causes. The work is admittedly preliminary and many of the interpretations are to be taken as tentative.

Procedure and Methods

This paper presents the results of exploratory studies carried on from time to time during the past two decades. The earlier field work, during the summer of 1931, was done near Lesser Slave Lake and in the older settled parts of the southern Peace River region. Later studies, especially those of the years 1947–50, were somewhat more intensive in nature and extended along the Mackenzie highway to the more northern parts of the region, also to the vicinity of Fort Vermilion and to the southern fringe of the Caribou Mountains. The method of investigation was that of reconnaissance combined with rather close study of selected samples. The areas for the more detailed studies were chosen with a view to securing floristic data for the region as a whole as well as for stands of various ages and conditions.

Though enormous areas of the region remain unexplored and though the samples of each community are relatively few, our general reconnaissance leads us to believe that these samples are fairly representative. Stands of different sizes were utilized, depending on circumstances or on some particular objective. For several of the stands quadrat studies of different kinds were carried out, but these have not been reported in the paper, with the exception of Table III. Records were usually made in the form of a species list, with prevalence noted by use of the following symbols: *d*, dominant; *ld*, locally dominant; *a*, abundant; *la*, locally abundant; *f*, frequent; *s*, scattered; *o*, occasional; *r*, rare. These records are presented in tabular form for the leading communities. It should be pointed out that the data are more complete, or even more accurate, for some stands of a particular community than for others. Especially for the bryophytes and lichens of the different communities is this so. Due account has been taken of these discrepancies in classifying and interpreting the vegetation.

The White Spruce Association

This association, dominated by *Picea glauca*, is one of the most prevalent and also one of the best defined plant communities of northwestern Alberta. Moreover, it is considered to be the climax association of the region. The characteristic white spruce of Alberta is generally regarded as *Picea glauca* var. *albertiana* (S. Brown) Sargent. However, there is considerable evidence that typical *Picea glauca* is not uncommon, and that it merges with the variety in some parts of our region. Until further study has been given to this taxonomic problem, we prefer to use the designation *Picea glauca*.

Of 12 stands of this association to which close study has been given, eight have been selected for presentation (Table I). These eight stands are widely scattered in the region, which is about 350 miles north to south and 200 miles across. They represent a fairly wide range in environmental conditions and traverse the boreal–cordilleran transition region from the Lesser Slave Lake stand (with *Abies balsamea*) on the east to the Dawson Creek stand (with *Pinus contorta* var. *latifolia*) on the west. Nevertheless, these examples of the association show a remarkable similarity in general ecological structure and in floristic composition.

Though the entire white spruce vegetation of the region is treated as a single plant association, a number of variations (faciations) may be recognized. Of these faciations the following are the most marked and also the most prevalent.

1. *Needle cover faciation*, the spruce being extremely crowded, the associated vegetation very sparse, and the ground cover composed chiefly of spruce needles. This aspect is presented by relatively young stands that have arisen through prolific spruce regeneration following a complete burn.

2. *Grass-shrub faciation*, characterized by the pine grass, *Elymus innovatus*, by *Aster conspicuus*, and various shrubs, notably *Shepherdia canadensis* and *Alnus crispa*. This type is common on steep slopes and on other dry or poor sites and may be regarded as an edaphic climax.

3. *Shrub–herb faciation*, having a prominent shrub stratum characterized by *Viburnum edule*, *Rosa* spp., and *Ribes* spp., and luxuriant herb strata with the following leading species: *Linnaea borealis* var. *americana*, *Rubus pubescens*, *Mertensia paniculata*, *Fragaria* spp., *Pyrola* spp., *Epilobium angustifolium*, *Calamagrostis canadensis*, *Cornus canadensis*, *Mitella nuda*, *Viola renifolia*, and *Petasites palmatus*. This faciation usually has a strong admixture of aspen and balsam poplar, as well as willows, especially *Salix bebbiana*, and often has some paper birch, while the spruce is generally not crowded. It is commonly found on sites with good soil and moisture conditions. In older stands spruce regeneration is usually good. There is considerable evidence that this type of spruce vegetation relates to partial or occasional burning of the area, the poplar being thus perpetuated and yet tending to favor a large measure of spruce regeneration.

4. *Feather moss faciation*, having an almost continuous carpet of *Hylocomium splendens*, *Calliergonella schreberi*, and other mosses, with which are associated

horsetails (*Equisetum* spp.), the bunchberry (*Cornus canadensis*), and various other species. The spruce of this faciation forms a fairly close canopy that admits sufficient light for the feather mosses and also provides ideal moisture conditions for these plants. Most shrub and herbaceous species are apparently unable to grow under the canopy, either because of insufficient light or because they cannot compete with the highly successful mosses. This faciation is probably to be regarded as the association climax (Clementsian sense); for, in the absence of burning, the other faciations tend to develop into the feather moss type, the spruce gradually supplanting the shorter-lived poplar and birch, while most shrubs and herbs are replaced by mosses. On the other hand, it seems doubtful whether this faciation is self-perpetuating as such, either following burning or subsequent to old age and decadence of the spruce. This is a problem requiring further investigation.

These faciations of the white spruce association intergrade to form various mixtures, depending upon the terrain, the age, and density of the spruce, and the past history of the area, especially in terms of burning. Of quite common occurrence are mixtures of the shrub–herb and feather moss faciations. Examples of several of these variants are provided by the stands reported in Table I and described below.

For the eight samples of the white spruce association shown in Table I, some 107 vascular plants and 24 mosses and lichens are recorded. In four other stands of this association an additional nine species were noted: *Senecio eremophilus* Richards., *Orchis rotundifolia* Banks, *Habenaria obtusata* (Pursh) Richards., *Listera borealis* Morong, *Ranunculus lapponicus* L., *Carex gynocrates* Wormskj., *Castilleja raupii* Pennell, *Impatiens* sp., and *Oplopanax horridus* (J. E. Sm.) Miq. Thus, for all the white spruce samples approximately 116 species of vascular plants have been recorded.

Following are brief characterizations of the eight stands for which species are listed in Table I.

The first sample (Table I), located some 25 miles north by northeast of Fort Vermilion, near the base and on a lower slope of the Caribou Mountains, is a well developed and fairly dense stand, the larger trees being about 100 ft. tall and 2 ft. d.b.h.† (Fig. 2). Two main aspects of the association, related to local edaphic conditions, are evident: (1) a feather moss faciation, with a nearly continuous mat of mosses, composed chiefly of *Hylocomium splendens*, with an abundance of *Equisetum* spp. and *Vaccinium vitis-idaea* var. *minus* on the lower and more moist parts of the area; (2) a grass–shrub faciation, characterized by *Elymus innovatus*, *Aster conspicuus*, *Shepherdia canadensis*, *Alnus crispa*, and *Rosa* spp. on the drier parts of the area.

The second area, located at the Alberta–Northwest Territories boundary, is dominated by spruce about 95 years old, but has considerable aspen locally and some regeneration of spruce, especially under the aspen. The stand is characterized by a nearly continuous mat of *Hylocomium splendens* and

† *d.b.h. = diameter at breast-height, 4.5 ft. from the ground.*

FIG. 2. White spruce (*Picea glauca*) association at the base of a south slope of the Caribou Mountains, northern Alberta.

FIG. 3. Mixed pine (*Pinus banksiana* and *P. contorta* var. *latifolia*) vegetation on a sandhill slope, south of Grande Prairie. Open area in the stand with conspicuous lichen cover.

FIG. 4. Small plants of the devil's-club (*Oplopanax horridus*) with the ostrich fern (*Pteretes pensylvanica*). Balsam fir (*Abies balsamea*) in the background. Near Lesser Slave Lake.

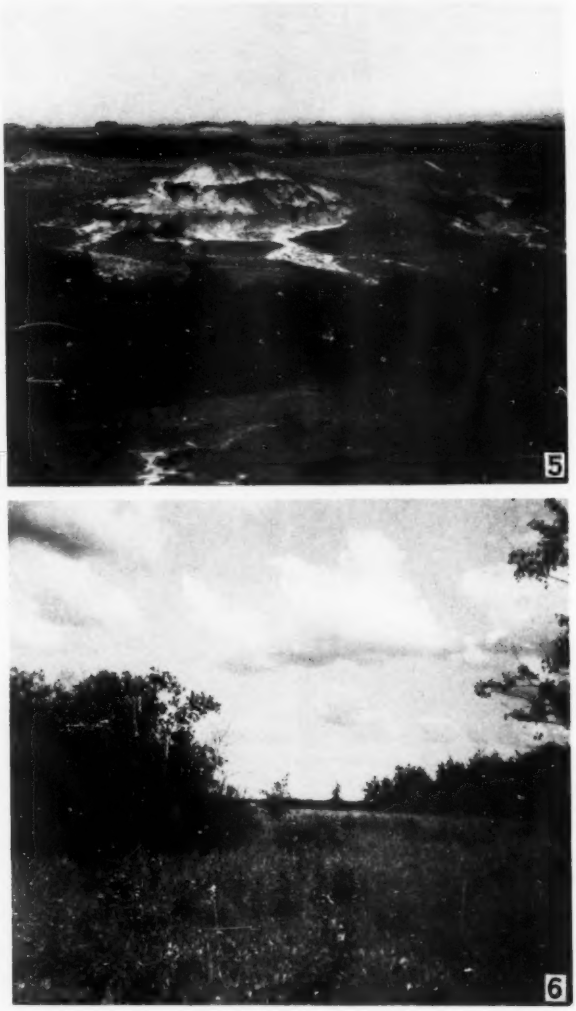

FIG. 5. Parkland between Grande Prairie and the Smoky River, with groves of trees and patches of natural grassland. In the center of the picture appear eroded slopes and flats of a badland area.

FIG. 6. Flat parkland, near Sexsmith, north of Grande Prairie. The aspen poplar is extending into the prairie grassland as root-suckers at the grove margins.

associated species, notably *Cornus canadensis*, *Vaccinium vitis-idaea* var. *minus*, *Equisetum* spp., and *Geocaulon lividum*, also by the two shrubs, *Shepherdia canadensis* and *Viburnum edule*.

The third sample, situated 10 miles south of Notikewin, has spruce trees of different ages, including those of approximately 200, 130, and 100 years, also considerable aspen somewhat over 100 years in age. The shrub and floor strata vary with the density of the tree cover, from the needle-covered ground under crowded spruce and the continuous moss–herb carpet typical of the association, to the shrub–herb vegetation found in the more open portions of the stand. Prominent in the latter parts of the stand are *Viburnum edule*, *Alnus crispa*, *Linnaea borealis* var. *americana*, *Calamagrostis canadensis*, *Aralia nudicaulis*, *Rubus pubescens*, and *Epilobium angustifolium*.

The Saddle Hills sample includes spruce of approximately 70 and 100 years, and poplar somewhat over 70 years in age. The densely shaded parts of the stand have a ground cover of needles with some moss; the moderately shaded portions have a nearly continuous moss cover characterized by *Hylocomium splendens* and such flowering herbs as *Linnaea borealis* var. *americana*, *Mitella nuda*, *Petasites palmatus*, *Viola renifolia*, and *Cornus canadensis*; the more open parts of the stand have a mixed vegetation that includes *Alnus crispa*, *Viburnum edule*, *Rubus idaeus*, *Linnaea borealis* var. *americana*, *Aster conspicuus*, *Arnica cordifolia*, *Mertensia paniculata*, *Mitella nuda*, *Cornus canadensis*, with much *Calamagrostis canadensis* in moist depressions and *Elymus innovatus* on the drier and poorer terrain.

The High Prairie sample, dominated by spruce about 70 years old, has little but needle cover on the floor of the more dense parts of the stand, while elsewhere the ground cover consists of extensive moss mats (*Hylocomium splendens* and *Calliergonella schreberi* predominating) and an abundance of *Linnaea*. Leading associated species are *Viburnum edule*, *Rosa* spp., *Rubus pubescens*, *Cornus canadensis*, *Mitella nuda*, *Mertensia paniculata*, *Galium boreale*, *Viola renifolia*, *Petasites palmatus*, *Calamagrostis canadensis*, and *Maianthemum canadense* var. *interius*.

The Sturgeon Lake stand is characterized by spruce somewhat over 70 years in age, 80 to 90 ft. in height and the larger trees about 15 in. d.b.h. Poplar of about the same height as the taller spruce, white birch of medium size, and numerous small spruce are scattered throughout most parts of the stand. The leading shrubs are *Salix bebbiana*, *Cornus stolonifera*, *Viburnum edule*, and *Lonicera involucrata*; the chief herbs include *Linnaea*, *Cornus canadensis*, *Maianthemum*, *Aster conspicuus*, and *Rubus pubescens*, while the moss stratum has an abundance of *Hylocomium* and *Calliergonella*.

The Lesser Slave Lake area, located at Widewater, on the south side and near the east end of the lake, differs from the other areas in the presence of balsam fir, *Abies balsamea*. There is also a considerable amount of aspen, as well as scattered balsam poplar, and white birch. Good regeneration of spruce and fir is indicated by numbers of young trees of these species. Shrub and herb strata are well developed, a fact that evidently relates to the good

light and moisture conditions, as well as the fertile soil, of this stand. Leading species include *Cornus stolonifera*, *Viburnum edule*, *Rosa* spp., *Cornus canadensis*, *Linnaea*, *Mertensia paniculata*, *Mitella nuda*, *Calamagrostis canadensis*, *Pyrola asarifolia*, *Aralia nudicaulis*, and *Hylocomium splendens*.

The Dawson Creek stand is unique among the spruce samples recorded in Table I in having lodgepole pine, *Pinus contorta* var. *latifolia*. This stand is located about 25 miles west of Dawson Creek, British Columbia. Both spruce and pine are 100 to 110 years old. The tall, straight trees form a dense stand, the spruce being dominant, the pine scattered to locally abundant. Characteristic of the stand is a moss mat composed of the usual "feather" mosses. Leading associated species are *Vaccinium vitis-idaea* var. *minus*, *Ledum groenlandicum*, *Elymus innovatus*, *Aster conspicuus*, *Cornus canadensis*, *Linnaea borealis* var. *americana*, *Petasites palmatus*, and *Peltigera aphthosa*.

Discussion

The white spruce association of our region bears a close resemblance to that of central Alberta for which a brief descripton has been published (9). These associations are shown to have practically the same leading species for all strata, as well as numerous secondary species in common. They may be regarded, therefore, as one and the same plant community, a *Picea glauca* association that extends throughout central and northwestern Alberta.

Raup (15, 17) has provided a good account of the white spruce forests of northeastern Alberta and adjacent Mackenzie region. Three divisions of these forests are recognized, namely, parklike white spruce, flood plain spruce, and upland mesophytic spruce. The first of these types consists of open parklike stands with little or no undergrowth but often with a ground cover of fruticose lichens and mat-forming shrubs. The drier phase of this forest as it occurs on sand is somewhat like the parklike white spruce vegetation described by the writer (9) for a sandhill area near Edmonton in south-central Alberta, though differing markedly in floristic composition. Parklike white spruce forest has not been seen by the writer in northwestern Alberta. Raup's flood plain and upland mesophytic spruce forests are evidently akin to the white spruce association of northwestern and central Alberta, the flood plain forest being somewhat like our shrub–herb faciation and the upland mesophytic forest resembling our feather moss faciation in structure and floristic content. A striking contrast between Raup's upland mesophytic spruce forest and our feather moss faciation is the large proportion of *Hypnum crista-castrensis* and the apparent absence of *Hylocomium splendens* in the moss carpet of the former.

Available information points to the conclusion that white spruce is the climax forest vegetation for mesic sites throughout northwestern Alberta and that burning is the chief factor impeding development of this climax. Though forest fires have been of common occurrence from time immemorial they have undoubtedly increased in our region since the advent of the white man, and tremendous areas of white spruce forest have become devastated recently. The subject of retrogression of spruce to poplar and pine following

various kinds of forest fires and subsequent return to spruce has been well described by Raup (17) for northern regions. The successional relationships of spruce and poplar have been discussed by the writer (9) for central Alberta. Foresters across the country have been interested in certain aspects of this subject, especially that of spruce regeneration under various edaphic conditions concerning which much research is still needed.

Black Spruce Association

Forest stands dominated by black spruce, *Picea mariana*, exhibit a number of phases and intergrade with certain other kinds of vegetation. Two main types, ranked as associations, are recognized for the region, viz. (*a*) black spruce – feather moss association, which intergrades locally with the white spruce association, (*b*) black spruce – bog moss association, regarded as a subclimax stage of a *Sphagnum* bog (muskeg) sere. Though these associations have many species in common, including the same dominant, they do show significant differences in floristic composition; moreover, they are unlike in respect to internal structure and generally in substratum, origin, and development.

Black Spruce – Feather Moss Association

This community might well be named a *Picea mariana – Hylocomium splendens* association, to denote the chief moss of the community. The dominant tree, black spruce, generally grows in close formation and is frequently accompanied by white spruce, aspen poplar, and various willows (*Salix* spp.). The floor is carpeted with "feather" mosses, notably *Hylocomium splendens*, while *Calliergonella schreberi* and *Aulacomnium palustre* are usually present, often abundant. More sporadic in occurrence are the mosses *Hypnum crista-castrensis*, *Camptothecium nitens*, and *Sphagnum capillaceum*. Accompanying the mosses are various lichens, notably *Peltigera aphthosa* and *Cladonia* spp. Associated species include *Ledum groenlandicum*, *Vaccinium vitis-idaea* var. *minus*, *Rosa* spp., *Ribes* spp., *Equisetum arvense*, *E. scirpoides*, *Cornus canadensis*, *Petasites palmatus*, *Linnaea borealis* var. *americana*, *Mitella nuda*, *Rubus pubescens*, and *Carex* spp. The four areas shown in Table II serve to illustrate the salient features of this association, as well as certain of its variants.

The Hythe stand is well carpeted with moss, below which are the following strata: a thin layer, 2–5 in. thick, of partially decomposed moss and wood; a layer, about 1 ft. thick, of rich black soil; a layer of stiff, gray to somewhat bluish clay. It appears that this area, originally occupied by a shallow lake, was long covered by marsh vegetation of sedges, grasses, and willows before the present community developed. Most of the area has a close stand of slender black spruce, with considerable white spruce intermixed locally, and an occasional tamarack. On the slightly higher and drier periphery of the area white spruce predominates. Circumstantial evidence indicates a succession to white spruce. The lower tree branches are well covered with the lichens *Usnea hirta* and *Parmelia saxatilis*. This stand differs from the

others (Table II) in the abundance of *Camptothecium nitens* and *Aulacomnium palustre* in the moss mat, though *Hylocomium splendens* is also prevalent. It is also unique in the abundance of horsetails and in the absence of ericads. Portions of the area recently burned or cleared are tenanted by mixtures of bog birch, willows, grasses, sedges, and broad-leaved herbs.

The Kinuso stand typifies the association in the prevalence of the three "feather moss" species and in most other respects. It is exceptional, however, in having considerable *Sphagnum*, though very little peat has been formed. The trees, somewhat over 60 years old, with a conspicuous growth of *Usnea* and other lichens on their branches, form a dense growth. While portions of the stand have needle-covered floor with sparse vegetation, most parts are carpeted with moss.

The stand on the Mackenzie highway, at the Alberta–N.W.T. boundary is also typical of the association. It is on a low, sandy area and shows no peat formation other than a thin layer of partially decomposed spruce needles, feather mosses, and lichens. The black spruce are of two ages, the younger being crowded and evidently produced since a burn of some 30 years ago. Below these crowded spruce is needle cover with occasional moss and lichen mats. The older and less dense parts of the stand have an almost continuous feather moss carpet, accompanied by much *Vaccinium vitis-idaea* var. *minus*, patches of *Peltigera* and a liverwort (*Ptilidium* sp.), and occasional clumps of *Ledum* and *Empetrum*.

The Steen River stand, although dominated in most parts by black spruce, has a large admixture of white spruce and some aspen; yet the associated vegetation is, in the main, that of the black spruce – feather moss association. An exceptional feature, found in drier and more open parts of the stand, is an abundance of *Elymus innovatus*, which is suggestive of the grass–shrub faciation of the white spruce association and may indicate a transition to that type. In fact, there is evidence in this stand of succession to different faciations of the white spruce association. It may be, however, that the trend is in the opposite direction, i.e. succession of white spruce to black spruce, as Kabzems (7) reads the evidence for forests in Saskatchewan. The stand is a rather open one, with the larger trees about 85 years old, 70 ft. tall, and about 12 inches d.b.h. The spruce overtop the aspen which are some 60 ft. in height. Quadrat records (Table III) for a representative portion of the stand show the prevalence of *Hylocomium splendens* in the ground cover, and the rather sporadic occurrence of most other species. The quadrats, one meter square, were taken along a transect at about 10 m. intervals in such a way as to exclude the trees. Ground coverage is shown in percentages. The records in Table III are not characteristic of the association as a whole; they serve rather to portray a particular variant of the association. They serve also to indicate the inadequacy of a limited number of quadrats for descriptive purposes. While such records do give a fairly clear picture of certain aspects, e.g. moss cover, they fail to set forth other significant features that a general inspection reveals.

Black Spruce – Peat Moss Association

In technical language, this is a *Picea mariana – Sphagnum* association. As the subclimax of a peat bog or muskeg sere, it may be called a bog forest or a muskeg forest. The dominant black spruce is usually less crowded than in the former association. The most common tree associates are tamarack, paper birch, and certain willows. The floor is characterized by bog mosses, especially *Sphagnum capillaceum* and *S. fuscum* and by species of *Cladonia*. Certain mosses, *Hylocomium splendens*, *Aulacomnium palustre*, and *Polytrichum juniperinum* occur sporadically. The most common flowering plants are *Ledum groenlandicum*, *Vaccinium vitis-idaea* var. *minus*, *Rubus chamaemorus*, and *Smilacina trifolia*. Less constant species include *Betula glandulosa*, *Vaccinium oxycoccos*, *Equisetum sylvaticum*, *Eriophorum spissum*, and *Carex* spp. The most striking structural feature of this community is the uneven floor of *Sphagnum* mounds and the nearly continuous cover of the low shrub, *Ledum groenlandicum*, commonly known as Labrador tea.

The first example, Steen River (Table II), is actually not typical of the black spruce – bog moss association, for it has been greatly altered by burning and shows now only scattered mounds of growing *Sphagnum* on the peaty substratum. The higher and drier parts of the stand exhibit a succession to *Hylocomium splendens* and *Equisetum sylvaticum*, while the lower, wetter areas, show a retrogression to *Betula glandulosa*, *Myrica gale*, *Salix*, *Larix laricina*, *Rubus acaulis*, *Calamagrostis*, and *Carex*. The older spruce and tamarack, on the unburned areas, are about 90 years in age, the spruce being only 30 to 40 ft. tall, the tamarack 45–50 ft. in height.

The Mackenzie, Grimshaw, and Fort St. John stands are regarded as typical of the association. They are well developed forests of black spruce, with festoons of *Usnea* from the lower branches and the floor characterized by *Sphagnum* mounds with *Ledum groenlandicum*, *Vaccinium vitis-idaea* var. *minus*, *V. oxycoccos*, *Rubus chamaemorus*, *Eriophorum spissum*, and *Cladonia* spp. The Fort St. John area has a central lake, showing different stages of a bog sere between its margin and the surrounding bog forest. Further discussion of the subject of bog development is reserved for a forthcoming paper on bogs and marshes of the region.

In addition to the species listed in Table II for the black spruce – peat moss association, the following have been recorded: *Lonicera villosa* (*Michx.*) R. & S. var. *solonis* (Eat.) Fern, *Gaultheria hispidula* (L.) Bigel., *Moneses uniflora* (L.) A. Gray, *Ranunculus lapponicus* L., *Carex disperma* Dewey, *Orchis rotundifolia* Pursh, *Spiranthes romanzoffiana* Cham., and *Vaccinium uliginosum* L. var. *alpinum* Bigel., the latter species found only on the south side of the Caribou Mountains.

Discussion

For all samples of the black spruce vegetation approximately 94 vascular plants and 25 bryophytes and lichens have been recorded. These figures compare with 116 vascular plants and 24 lower plants identified in the white spruce association.

Floristically, the black spruce – feather moss association differs from the black spruce – peat moss association in its floor carpet of "feather mosses" rather than of *Sphagnum* and in having numerous species, variously disposed, rather than a small number of constant and very prominent species, notably *Ledum groenlandicum* and *Vaccinium vitis-idaea* var. *minus*. Structurally, the fairly even and firm (though moss carpeted) floor of the first association contrasts with the mounded, soft floor of the second association; and the patchwork of life forms found in the first contrasts with the nearly continuous *Ledum* shrub and *Sphagnum* mound strata of the second community.

The black spruce – feather moss association seems generally to have developed on quite shallow depressions, or fairly level terrain, through sedge–grass–willow stages and without much peat formation. In contrast, the black spruce – peat moss association has arisen in deeper depressions, through acid bog (muskeg) stages and with the production of a considerable thickness of *Sphagnum* peat. This association is interpreted as a subclimax community, maintained as such by prevailing edaphic conditions and by periodic burning. Natural succession is to a black spruce – feather moss community, for there is abundant evidence in many of the drier bog forests, of the replacement of *Sphagnum* and *Ledum* by feather mosses, *Equisetum*, *Linnaea*, and other plants of this community. But this trend is quite generally offset by the pyric factor, which brings about retrogression to earlier stages of the bog forest sere, through destruction not only of the vegetational cover but also of the upper peat layers.

Whether there is a natural succession of the black spruce – feather moss association to the white spruce association is somewhat problematical. The writer's idea of white spruce as climax for the region appears to be challenged by the recent work of Kabzems (7). For certain areas in Saskatchewan, Kabzems states that the more vigorous black spruce succeeds the white spruce. However, in our region the black spruce – feather moss association is probably to be interpreted as an edaphic climax, being long maintained as such by poor drainage and also by periodic burning.

It may be noted here that black spruce does occur apart from the two associations already described. Especially in the more northern parts of our region, black spruce is rather common in pine and other wooded stands on many kinds of terrain. For example, near the Alberta–N.W.T. boundary black spruce was found, on rather sandy soil and level terrain, in pure stands and also intermixed in various proportions with aspen poplar and jack pine. Such vegetation seems to defy recognition of communities, whether in terms of tree dominants or of associated species. Reference may also be made to black spruce on the upper slopes and on dry summits of the Caribou Mountains where it grows in pure stands and also intermixed with lodgepole pine. In certain places this vegetation conforms to our black spruce – feather moss association; but, elsewhere quite different features are presented, for example a somewhat open stand with shrub and herb strata characterized by *Alnus*

crispa and *Elymus innovatus* respectively. These aspects of the black spruce vegetation will be given further consideration in the latter part of the paper.

Comparison may be made with black spruce vegetation in contiguous areas. The so-called "young bog forest" reported (8) for central Alberta conforms closely to our black spruce – bog moss association; and the "mature bog forest" described for that region as climax forest is similar to our black spruce – feather moss association. For the Athabaska – Great Slave Lake region Raup (17) describes bog forest having a wet phase characterized by *Sphagnum* and a dry condition "with woodland species of *Hypnum*". These phases evidently correspond to our two black spruce associations. There are, however, striking differences in the secondary species of the bog forests of the Mackenzie valley and northwestern Alberta. Even for different parts of the former region Raup reports marked variations in the secondary species of bog forest. Raup's account of black spruce near the top of the eastern slope of the Caribou Mountains is corroborated by our observations on southern areas of these mountains. Raup describes pure stands of black spruce and also black spruce – lodgepole pine mixtures, with different kinds of floor and shrub strata. Of interest too is Raup's report that mixed forests of black spruce, lodgepole pine, and white spruce are widespread along the Alaska Highway beyond Fort St. John, British Columbia.

Tamarack (Larch) Vegetation

Though dominated by tamarack, *Larix laricina*, this vegetation is ecologically and floristically similar to the black spruce – peat moss association. Like the latter, it develops on a peaty substratum, as a subclimax stage of a bog sere, and has a floor of peat-forming mosses. The main differences relate to the fact that the tamarack establishes in a *Drepanocladus–Carex–Betula* bog which continues in a relatively wet condition. *Sphagnum* mosses often invade this type of bog, developing there along with the tamarack. The extent of *Sphagnum* development is affected by the size of the bog, by periodic flooding, and by burning. With the growth of *Sphagnum* mounds, conditions become more favorable for black spruce and ericads but less suited to tamarack, sedges, and certain other plants of the tamarack vegetation. Our observations on tamarack are in accord with those of Beeftink (1), who states that this plant is very intolerant of shade and can not succeed in competition with Labrador tea and other plants that soon cover the enlarging *Sphagnum* mounds, while black spruce flourishes under these conditions. Thus, succession to the black spruce – peat moss association may take place. Following this, in turn, there may be a succession to the black spruce – feather moss association. Earlier stages in bog development will be described in a forthcoming paper; only those later stages, involving tamarack and spruce, are considered here.

Because of the complexity of factors affecting its development and perpetuation, tamarack vegetation exhibits many aspects. Certain of these aspects are illustrated by a few selected tamarack stands, descriptions of which follow.

A tamarack stand, located north of Hondo, near Smith, forms a portion of a bog area surrounding a small lake. Evidently the tamarack association has developed on *Drepanocladus–Carex* bog which, in turn, arose at the lake margin. This bog will be described in a forthcoming paper. The tamarack stand, with trees some 30 ft. tall, has an understory of low shrubs, chiefly *Betula glandulosa* and *Salix pedicellaris* var. *hypoglauca*, and a floor covering of the mosses, *Camptothecium nitens* and *Aulacomnium palustre*, with a few pools of water throughout. Associated with the mosses are numerous vascular plants, including *Vaccinium oxycoccos*, *Rubus acaulis*, *Galium labradoricum*, *Potentilla palustris*, *Caltha palustris*, *Equisetum palustre*, *Menyanthes trifoliata*, and *Carex* spp.

A second stand, located near Hondo and Smith is dominated by tamarack trees some 50 ft. tall, about 12 in. d.b.h. and 80 years old. Younger tamarack are intermixed and black spruce occurs locally. There is an understory of rather tall bog birch, *Betula glandulosa*, and willows, chiefly *Salix bebbiana*. The floor is very uneven, because of timber fall and large moss mounds, composed mainly of *Sphagnum magellanicum*. The *Sphagnum* mounds are overgrown by feather mosses, especially *Hylocomium splendens* and by Labrador tea, sedges, cranberries (*Vaccinium* spp.), and other plants. Between the mounds there are coarse grasses and sedges, also *Equisetum limosum*, *Potentilla palustris*, and *Caltha palustris*. These species have evidently persisted from earlier stages in bog succession. Despite these relicts of wetter conditions, the stand has developed to a relatively dry stage, almost too dry in fact for *Sphagnum* growth, and there is evidence of succession to a feather moss floor cover.

A stand, located near the Wapiti River, almost six miles south of Grande Prairie, is dominated by tamarack trees about 95 years old, 40 ft. tall, and 12 in. d.b.h. Black spruce of about the same age as the tamarack are scattered throughout most parts of the stand. Some cutting out of tamarack was done many years ago and again recently. Regeneration of tamarack has been very good and many of the younger trees are 12 to 15 ft. in height. Associated with the younger tamarack in the understory are willows and bog birch. On the floor are moss mats and mounds, interspersed by pools of water. The chief mosses are *Aulacomnium palustre*, *Camptothecium nitens*, *Sphagnum recurvum*, and *S. fuscum*. Associated with the mosses are *Vaccinium oxycoccos*, *V. vitis-idaea* var. *minus*, *Ledum groenlandicum*, *Smilacina trifolia*, *Geocaulon lividum*, *Orchis rotundifolia*, and several small species of *Carex*. In the pools are *Equisetum limosum*, *Potentilla palustris*, *Carex lasiocarpa* var. *americana*, *C. rostrata*, and *Calamagrostis inexpansa*. This stand merges locally with nearly pure stands of black spruce, characterized by *Sphagnum*, *Ledum*, and *Vaccinium*, i.e. there is an easy transition of the tamarack vegetation to the black spruce – peat moss association. Occasional large tamarack occur in the black spruce areas. Natural succession of tamarack to black spruce is clearly indicated.

A tamarack area, situated near the east end of Lesser Slave Lake is similar to the last stand in many respects but differs in having considerable alder and

paper birch and also *Chamaedaphne calyculata* associated with Labrador tea. Bordering some of the small pools and associated with *Aulacomnium* and *Potentilla palustris* are *Sphagnum capillaceum*, *S. palustre*, and *S. squarrosum*. The creeping snowberry, *Gaultheria hispidula*, occurs locally on *Sphagnum* mats.

A tamarack stand located near Steen River, some 300 miles farther north than any of the other areas noted, shows features similar to these, with the addition of certain 'northern' species, namely, *Myrica gale* (in quite wet situations), *Arctostaphylos rubra*, and *Potentilla fruticosa*, the last two species occurring in drier parts of the stand.

Tamarack (Larix laricina) Association

Our study of the foregoing stands and other similar samples points to the recognition of a *Larix laricina* association for the region. Structurally, this association is characterized by a single tree dominant, the tamarack, often with black spruce interspersed; a shrub stratum, usually consisting of bog birch and a number of willow species; an uneven floor with scattered pools of water and with wet mats and mounds formed of various mosses; associated with the mosses are low, creeping shrubs, small sedges, and several broad-leaved herbs; occurring sporadically are low, erect shrubs, tall herbaceous species, and coarse horsetails (*Equisetum*), grasses, and sedges. The floristic composition of the association may be set forth as follows:

	Woody plants		
Larix laricina	d	*Vaccinium oxycoccos*	s,la
Picea mariana	o,la	*Vaccinium vitis-idaea* var. *minus*	o
Betula glandulosa	f,la	*Ledum groenlandicum*	o,la
Betula papyrifera	r	*Chamaedaphne calyculata*	r
Alnus rugosa var. *americana*	r	*Arctostaphylos rubra*	r
Salix pedicellaris var. *hypoglauca*	o,la	*Gaultheria hispidula*	r
Salix bebbiana	s	*Ribes hudsonianum*	o
Salix candida	o	*Ribes hirtellum*	r
Salix discolor	o	*Lonicera involucrata*	r
Salix glauca	r	*Lonicera villosa* var. *solonis*	r
Salix myrtillifolia	r	*Potentilla fruticosa*	r
Salix maccalliana	r	*Myrica gale*	r
Salix pyrifolia	r		
	Herbs		
Carex disperma	s	*Caltha palustris*	s
Carex lasiocarpa var. *americana*	o	*Galium trifidum* }	o,la
Carex rostrata	o	*Galium labradoricum* }	
Carex aquatilis	o	*Rubus acaulis*	o,la
Carex gynocrates	o	*Rubus pubescens*	o
Carex leptalea	o	*Menyanthes trifoliata*	o
Carex capillaris	o	*Smilacina trifolia*	o
Carex heleonastes	o	*Stellaria* spp.	o
Carex vaginata (*C. saltuensis*)	r	*Petasites sagittatus*	o
Carex tenuiflora	r	*Orchis rotundifolia*	r
Carex chordorrhiza	r	*Habenaria obtusata*	r
Carex prairea	r	*Senecio pauperculus*	r
Carex paupercula	r	*Pyrola asarifolia* var. *purpurea*	r
Carex media	r	*Cardamine pennsylvanica*	r
Calamagrostis spp.	s	*Pedicularis labradorica*	r
Equisetum limosum	s	*Moneses uniflora*	r
Equisetum arvense	o	*Ranunculus lapponicus*	r
Equisetum palustre	r	*Chrysosplenium iowense*	r
Potentilla palustris	s		

Bryophytes

Aulacomnium palustre	f, la	*Sphagnum recurvum*	o,la
Camptothecium nitens	f,la	*Sphagnum magellanicum*	o,la
Drepanocladus spp.	o,la	*Sphagnum capillaceum*	o,la
Hylocomium splendens	o,la	*Sphagnum fuscum*	o,la
Calliergonella schreberi	o	*Sphagnum tenerum*	r
Hypnum crista-castrensis	r	*Sphagnum squarrosum*	r
Mnium spp.	o	*Sphagnum palustre*	r
Polytrichum spp.	o	*Sphagnum girgensohnii*	r
Dicranum spp.	r	*Ptilidium* spp.	r

Balsam Fir Vegetation

Balsam fir (*Abies balsamea*) has been mentioned as a member of a white spruce stand growing near Widewater, Lesser Slave Lake. In that region, this species is not uncommon, occurring generally in mixed stands of white spruce, aspen, balsam poplar, and white birch, only locally in nearly pure stands. It grows mainly on flat areas and gentle slopes south and southeast of the lake. It occurs also on sand dunes at the east end of Lesser Slave Lake and on Dog Island near the same end of the lake. Associated species are those commonly found in the white spruce and poplar associations of the region. Near Widewater and on Dog Island an interesting associated species is the devil's-club, *Oplopanax horridus* (Sm.) Miq. Small plants of this species, growing with the ostrich fern, *Pteretis pensylvanica* (Willd.) Fern., in a low, wet place in fir–spruce–poplar–birch woods, are shown in Fig. 4.

Though balsam fir is prevalent near Lesser Slave Lake, it is rare for the region as a whole. We observed a few trees of balsam fir in a mixed stand on the Saddle Hills and are informed that fir occurs near the Smoky River and Sturgeon Lake. Whether all the balsam fir of our region is to be assigned to *Abies balsamea* is doubtful. The alpine fir, *Abies lasiocarpa* (Hook.) Nutt., has been reported for Lesser Slave Lake (perhaps in error) and for the Swan Hills, south of Lesser Slave Lake. Confusion as to the identity of the balsam fir in the region of Lesser Slave Lake prevails also in respect to fir well to the south of that region, for example, near Whitecourt on the Athabasca River, and at Pigeon Lake and at Battle Lake, some 50 miles southwest of Edmonton. A recent study by Dr. G. H. Turner and the writer points to the conclusion that the fir at Battle Lake may be assigned to *Abies lasiocarpa*, though some of the trees approach *A. balsamea* rather closely. Further attention should be given to the ranges of the two species of *Abies* in Alberta and to the question of intergrading of these species.

Pine Vegetation

Earlier reports (6, 11) on the jack pine (*Pinus banksiana*) and the lodgepole pine (*P. contorta* var. *latifolia*) of northwestern Alberta show (*a*) that the ranges of these species overlap in the southern part of the region and that numerous intermediates (hybrids) between the species occur there, (*b*) that the ranges of these pines separate northward, with a broad area between them lacking pine, except for two isolated outliers of lodgepole. Our recent studies

of forests along the northern portion of the Mackenzie highway reveal that pine is actually quite prevalent there, that jack pine predominates, that typical lodgepole is rare and that intermediates (hybrids) between the two species are numerous. Therefore, the line showing the western limit of jack pine should be drawn at least as far west as the Mackenzie highway in the northern corner of Alberta. Our studies show that jack pine predominates near Fort Vermilion, with an admixture of intermediate types, and substantiate earlier reports of lodgepole pine on the Caribou Mountains.

The pine vegetation of the region, while usually found on sandy and gravelly areas, occurs also on heavier soils especially westward where lodgepole predominates. The sandy hills and ridges supporting pine vegetation exhibit sharp changes in edaphic conditions and in microclimate, with corresponding marked variations in floristic composition and ecological structure of the vegetation. Classification in terms of vegetational types is therefore difficult and somewhat arbitrary. For our purpose the pine vegetation of the region will be treated as an association. Within this association, two consociations may be recognized, the jack pine and lodgepole consociations, on the basis of species dominance. For each of the consociations, a number of faciations may be distinguished by their ground cover. Of these faciations, two are quite prevalent and rather well defined, (*a*) ***Pine – feather moss faciation***, characterized by *Hylocomium splendens* and *Calliergonella schreberi*, along with various higher plants such as *Linnaea*, *Pyrola* spp., *Cornus canadensis* and found on the more moist and more shaded sites, (*b*) ***pine–heath faciation*** characterized by *Arctostaphylos uva-ursi*, *Vaccinium vitis-idaea*, *Elymus innovatus*, *Oryzopsis pungens*, *Polytrichum* spp., *Cladonia* spp., and developed on the drier and more open parts of stands. Several species, including *Alnus crispa*, *Rosa* spp., *Salix* spp., and *Maianthemum* are common to both faciations. These and certain other variations of the pine association are illustrated by the sample stands of Table IV.

Near Smith the pine vegetation, a jack pine consociation, occupies the tops and slopes of sand ridges and hills that alternate with boggy depressions. The trees of the area studied are about 32 years old and average about 46 ft. in height and 6 in. d.b.h. The associated vegetation on the higher and drier portions of the area is mostly sparse and conforms to the pine–heath faciation. The vegetation on the relatively few moist slopes of the area is referable to the pine – feather moss faciation. This faciation merges with various kinds of bog vegetation near the base of the sandy slopes and bordering the depressions. Large portions of the ridges and hills are without tree vegetation or with only scattered trees. The vegetation of these open areas approximates to the pine–heath faciation, but with a greater proportion of *Polytrichum piliferum*, *Cladonia* spp. and other lichens, small grasses and sedges, and several broad-leaved plants, including *Rosa woodsii*, *Pulsatilla ludoviciana*, *Anemone multifida* var. *hudsoniana*, *Solidago* spp., *Artemisia caudata*, and *Hieracium umbellatum*. This vegetation, characterized by light-demanding and drought-

resisting plants, has evidently developed on pine areas that have been severely burned and that may again become dominated by pine. It may therefore be called a pine–heath associes.

At Peace River the pine association is dominated by typical jack pine, with an admixture of trees showing lodgepole affinities. It occupies a gently undulating area near the river where the soil is sandy and underlain by gravel. Most of the trees are about 65 years old, 80 ft. tall, and 8 in. d.b.h. Locally there are older trees, approximately 80 years in age and 12 in. d.b.h. In open portions of the area there are young pines of various ages and also a few young white spruce. Pine – feather moss and pine–heath faciations may be recognized, though they tend to merge on the relatively level terrain of this area. Prominent in the feather moss mats and also in the extensive carpets of bearberry, *Arctostaphylos uva-ursi*, is the fruticose lichen, *Cladonia mitis*.

The Grande Prairie area, located near the Wapiti River, consists of sand hills and ridges, with associated bogs, similar in topography to the pine area near Smith. The trees are 90 years or more in age, 35 to 65 ft. tall, with diameters of 13 to 16 in. and form a fairly open stand (Fig. 3). Both jack and lodgepole pine, as well as several intermediate forms, are prominent in the area studied. Represented in the area are the pine – feather moss and the pine–heath faciations, the latter being by far the more prevalent. The pine–heath associes, as defined for the Smith area, is also prominent. The mistletoe, *Arceuthobium americanum*, is common in this area. Though not observed in any of the other stands of Table IV, the mistletoe was found at points near Lesser Slave Lake, on the Smoky River, and near Fort Vermilion.

On the Saddle Hills, the pine is lodgepole and generally has an admixture of white spruce, aspen, and balsam poplar, growing mostly on fairly heavy soil. The trees are about 60 years old, 40 to 60 ft. tall, with an average d.b.h. of about 12 inches. Leading associated species include *Arctostaphylos uva-ursi*, *Hylocomium splendens*, *Linnaea*, *Elymus innovatus*, and *Cladonia* spp. Thus there is a close approach to the pine – feather moss faciation.

The Hawk Hills area is also dominated by lodgepole pine, with a strong admixture of spruce and poplar locally. The area was severely burned somewhat more than 25 years ago, the young pines being about 25 years old, with a height of 20 to 30 ft. and an average d.b.h. of 5 in. There is a prominent understory of willows and alder (*Alnus crispa*), with white spruce and Canadian buffalo berry (*Shepherdia canadensis*) abundant locally. The spruce appear to be 10 to 12 years old. The willows, alder, and spruce have been severely damaged in recent years, probably by elk and rodents. Natural succession of pine to spruce is indicated, despite temporary slowing of the spruce through shading and animal damage. The general aspect of the stand is that of the pine–heath faciation. Open areas in the stand are characterized by *Cladonia* spp., *Peltigera canina*, and *Polytrichum* spp. on the floor.

Both of the British Columbia stands, Taylor and Fort St. John, belong to the lodgepole consociation. The Taylor stand, on a level area with brownish sandy soil, consists of straight, closely crowded trees, about 60 ft. in height

and 40 years old. There is a sparse understory of willow and spruce, the latter being not over 15 ft. tall, though almost as old as the pine. Much of the floor has needle cover, with patches of feather mosses, lichens, and *Linnaea*. Though the associated vegetation is mixed, there is an approach to the pine – feather moss faciation. The Fort St. John stand occurs on a gently undulating area with gray, somewhat sandy, soil. It has the aspect of heavy timber, the tall, straight trees being about 110 years old. The greater part of this forest shows the pine – feather moss faciation.

Discussion

As is well known, jack and lodgepole pines are fire trees, commonly reproducing by seed following burning of stands. Since they are also light-demanding, they succeed on burned areas because their early growth is much faster than that of any spruce that may have started. Moreover, they send their taplike roots deep into sandy and gravelly soils, making for success on apparently dry sites. On the other hand, they are rarely successful on the heavier and more impervious soils, partly because these soils are not readily penetrated by the taproot of the pine and partly because spruce and other competing trees, having shallow but efficient root systems, flourish on these sites.

The drier pine areas, such as tops and south-facing slopes of sand ridges, are generally occupied by the pine–heath faciation of the pine association or by widely scattered pine and the pine–heath associes. Where the pine–heath associes occurs, pine regeneration will lead to the development of the pine association. However, since both drought and burning militate against the success of pine on these drier areas, the pine–heath associes tends to persist there indefinitely and so may be regarded as an edaphic climax. On more moist pine sites, where the pine – feather moss faciation of the pine association tends to become climax, pine regeneration is generally good following burning and the association is gradually restored. However, in the absence of burning over a long period, succession to white spruce is likely to occur. Most pine areas have nearby stands of spruce, which sooner or later provide seed for the establishment of seedlings under the pine. As a pine stand thins out with advancing age, the shade-tolerant and longer-lived spruce overtop the pine to become dominant. With the decline of the pine and the ascendancy of the spruce, there is relatively little change in the associated vegetation. For the feather moss faciation of the white spruce association is quite similar to that of the pine association.

The jack pine consociation of northwestern Alberta is similar to the pine vegetation already described by Dowding (5) for sandhills of central Alberta. Dowding's "pine–moss association" for the more xeric sites is similar to our pine–heath associes, and her "pine–heath association" of mesic sandhill sites resembles our pine–heath faciation. Apparently our pine – feather moss faciation is not well represented in the areas described by Dowding. The "pine–birch association" of Dowding's paper is perhaps best treated, not as a community, but as transition vegetation between pine and bog associations.

In northwestern Alberta, similar transition vegetation, very mixed and variable in nature, occurs where sandhill bases and bog margins merge.

The jack pine vegetation of our region and that described by Raup (17) for areas in the Wood Buffalo Park and around Lake Athabasca have several features in common but show so many significant differences that they can hardly be included in the same plant community. Raup describes the jack pine vegetation of his region in two phases,—that on sandy plains or ridges, and that on rocky hills. The former phase is not unlike our jack pine association but differs in having *Picea mariana*, *Cladonia rangiferina*, and *Cetraria nivalis* as primary species, as well as such secondary species as *Empetrum nigrum*, *Vaccinium uliginosum*, *Panicum subvillosum*, *Cypripedium acaule*, *Cladonia alpestris*, and *Lechea intermedia* var. *depauperata*. It differs also in the remarkable paucity of species, especially of vascular plants, over large tracts of the vegetation.

Poplar Association

The aspen poplar, *Populus tremuloides*, is the most common tree of the region, forming pure stands and also growing intermixed with the other tree species. One of its associates, the balsam poplar (*P. balsamifera*), also occurs in nearly pure stands, especially on the more moist poplar sites such as river flats. In contrast with balsam poplar, aspen thrives over a wide range of edaphic conditions and is often found as the dominant species, even on areas that appear ideally suited to the former species. The entire poplar vegetation of the region is regarded as an association, within which aspen and balsam poplar consociations are recognized.

Balsam Poplar Consociation

The records (Table V) for this, the *Populus balsamifera* consociation, are for areas lying across the southern part of the region. Included are stands of various ages and on different kinds of substrata. The High Prairie sample is on a low, moist area with rich black soil. The older trees are close to 100 years old and have a prominent understory of smaller poplar, willow, and dogwood, below which is a luxuriant growth of herbaceous species. The Smoky River stand, on a flat area with alluvial soil, is characterized by poplars 60 to 70 ft. tall and about 12 in. near the base, a prominent small tree – tall shrub stratum consisting of alder and dogwood, a sparse low shrub stratum with roses, and a relatively poor showing of herbs and mosses. In contrast with the above, the Wanham stand is very young, being only 10 years old, having succeeded a former poplar stand after a severe burn. The Sturgeon Lake stand is on high land in a gray or "wooded" soil region. The dominant trees are about 50 years old, 60 ft. tall, and with a d.b.h. of nine inches. There is a well developed small tree understory composed of alder and willows and a conspicuous low shrub stratum in which *Viburnum edule* is exceptionally prominent. The Rolla sample is on a low, moist area with gray soil and includes considerable aspen and white spruce, also a few lodgepole pine. The poplar and spruce are approximately 40 years old, most of the spruce being

somewhat over half the height of the poplar. Succession to spruce is clearly indicated. On the floor of the area are large decayed logs with mosses and lichens in abundance. The Dawson Creek stand also includes considerable aspen and some lodgepole pine, the poplars being about 50 years old. The shrub strata, characterized by alders, willows, dogwood, and roses are prominent, as also are the herb strata, in this well developed sample of the poplar vegetation.

The internal ecological structure and floristic composition of the balsam poplar consociation may be summarized as follows: a prominent small tree – tall shrub stratum, with *Salix bebbiana*, *Cornus stolonifera*, and sometimes *Alnus rugosa* var. *americana;* a low shrub layer, consisting chiefly of *Rosa* spp., *Rubus idaeus*, and *Lonicera involucrata*; herb strata characterized by *Calamagrostis canadensis*, *Aster ciliolatus*, *Rubus pubescens*, *Mertensia paniculata*, *Fragaria* spp., *Equisetum* spp., *Epilobium angustifolium*, *Thalictrum venulosum*, *Galium boreale*, *Vicia americana*, and *Pyrola asarifolia;* mosses and lichens, rather sporadic, growing mainly on decaying wood of the forest floor and on tree trunks, *Pylaisia polyantha* being common on the basal parts and *Orthotrichum* at higher levels of the trunks; a total of 87 vascular species for the six areas of Table V, a number that would be greatly exceeded through more extensive studies of the consociation.

Aspen Poplar Consociation

Of the 20 samples of the *Populus tremuloides* consociation that have received close study, 10 are presented in Table VI. These samples occur over a wide geographical range (Fig. 1) and include a diversity of edaphic conditions as well as stands of various ages.

The Steen River area, located some 30 miles south of the Alberta–N.W.T. boundary, has sandy to gravelly soil and a mature, rather open stand of aspen, about 75 years old and 50 ft. tall, with scattered jack pine and white spruce. It is a relatively poor site for aspen growth. The 50-year pine, though much younger than the aspen, extend slightly above the aspen canopy. The spruce are relatively young but, in the absence of fires, seem destined to gain ascendancy over both aspen and pine and eventually, with continued regeneration, to dominate the area. The associated vegetation is exceptional for the aspen community, especially in the abundance of bearberry (*Arctostaphylos uva-ursi*), buffaloberry (*Shepherdia canadensis*), and pine grass (*Elymus innovatus*); these are indicators of the poorer aspen sites and the bearberry of sandy and gravelly soils.

The Fort Vermilion stand, on rather rich soil, consists of aspen of two ages, 55 and 25 years, indicating a partial burn of some 25 years ago. The larger trees have a height of about 60 ft. and a d.b.h. of 11 inches. The Keg River area is flat and has about 7 inches of heavy black top soil with brown clay and stiff bluish clay beneath. This area adjoins the Keg River prairie and almost certainly was at one time covered by *Agropyron–Carex* grassland, though there is no sign of any relicts of that vegetation. The trees are about 40 years old;

they reach a height of 55 ft. and a d.b.h. of 9 inches, growing in close formation. The associated vegetation is suggestive of the balsam poplar consociation, which is believed to reflect the good moisture conditions of the area.

The Notikewin stand lies several miles south of the Notikewin prairie region, on rather high ground with poor soil. This forest was studied in 1931 and again in 1950. The poplars, about 55 years old in 1950 had grown from about 25 ft. to 40 ft. during the previous 20 years, while the larger trees had increased from about 3.5 to only 5 inches d.b.h. This is evidently a poor area for aspen growth. The associated vegetation is believed to be fairly typical of the aspen consociation; however, the abundance of *Shepherdia* and *Elymus innovatus* is exceptional and indicative of poor site quality, as also is the large amount of bare ground. A marked decrease in moss–lichen ground cover has taken place during the past 20 years, especially in the lichen element. This evidently relates to a decrease in rotting wood on the ground; for, in 1931 there were numerous remains of large charred logs on which much of the moss–lichen growth was found.

The Nampa stand represents rather well the decadent condition of the consociation, where extensive thinning through age and disease of the aspen has taken place. The trees are somewhat over 70 years old and stand about 75 ft. high. There is evidence of extensive killing by *Fomes igniarius* and also of fire damage by partial burns that occurred about 35 and 55 years earlier. The good growth shown by the aspen and the evident vigor of the associated plants correlate with the dark soil and low flat terrain of this area. The High Prairie stand is also on a low-lying area with rich soil. The trees are about 50 years old and form a dense stand, while the associated plants are to be regarded as fairly typical of the community.

The Hythe stand is quite dense, being slightly more than 30 years old and having extensive charred and rotted remains of the parent stand on the floor. This decaying wood supports most of the abundant lichen, liverwort, and moss growth that is present. The sample at the Alberta – British Columbia boundary is also fairly young, being about 40 years old, and with numerous decaying logs on which various lichens and bryophytes thrive. The soil appears to be a podsolic clay, with sandy patches. Intermixed with the aspen are balsam poplar and a few lodgepole pine. The shrub and herb strata are fairly characteristic of the consociation. The Fort St. John stand is an old one, being about 110 years in age, and yet is fairly dense and composed of tall, straight, apparently vigorous trees. The ground vegetation is rather sparse, presumably because of the considerable shade below the close canopy.

For the 10 areas included in Table VI, 116 vascular species and 24 bryophytes and lichens are recorded. For 10 other stands, the following additional vascular species have been noted: *Corylus cornuta* Marsh, *Salix planifolia* Pursh, *S. myrtillifolia Anders.*, *Ribes lacustre* (Pers.) Poir., *Alnus rugosa* (Du Roi) Spreng. var. *americana* (Regel) Fern., *Galium triflorum* L., *Apocynum androsaemifolium* L., *Lycopodium annotinum* L., *Cinna latifolia* (Trev.) Griseb., *Impatiens noli-tangere* L., *Urtica gracilis* Ait., *Heracleum lanatum*

Michx., *Dryopteris disjuncta* (Rupr.) Morton, *Athyrium filix-femina* (L.) *Roth*, *Pteretis pensylvanica* (Willd.) Fern., *Chrysosplenium iowense* Rydb., and *Thalictrum sparsiflorum* Turcz. var. *richardsonii* (Gray) Boivin, the last nine of which occur in low, moist locations; also, the two mosses, *Orthotrichum* sp. and *Thuidium recognitum* (Hedw.) Lindb. Thus, a total of 133 vascular plants and 26 bryophytes and lichens have been recorded.

The salient features of the aspen poplar consociation that pertain to internal structure and floristic composition may be summarized as follows: a discontinuous small tree – tall shrub stratum characterized by willows, notably *Salix bebbiana*, other species such as *Cornus stolonifera* and *Amelanchier alnifolia* being quite sporadic; a rich low shrub stratum, characterized by *Rosa acicularis*, *R. woodsii*, and *Viburnum edule*, while others such as *Symphoricarpos albus*, *Shepherdia canadensis*, *Rubus idaeus*, and *Ribes oxyacanthoides* are important elements; herb strata characterized by *Cornus canadensis*, *Vicia americana*, *Lathyrus ochroleucus*, *Rubus pubescens*, *Galium boreale*, *Fragaria glauca*, *Epilobium angustifolium*, *Calamagrostis canadensis*, *Aster ciliolatus*, *Maianthemum canadense*, *Pyrola asarifolia*, *Elymus innovatus*, and *Agropyron trachycaulum*; sporadic mats of bryophytes and lichens on the forest floor, especially on decaying wood, and bands of *Pylaisia polyantha* very common on the tree trunk bases; a total of 133 vascular species and 26 bryophytes and lichens for the 20 stands investigated. It may be pointed out that many additional species of mosses and liverworts would have been recorded if attention had been paid to the less conspicuous members of these groups.

Relationships of the Poplar Association

For the entire poplar association, using the records secured for both consociations, approximately 150 species of vascular plants and 27 bryophytes and lichens have been cited. This compares with 178 vascular plants and 39 mosses and lichens recorded in a somewhat more intensive investigation of the poplar association of central Alberta (9).

Certain leading species of the poplar region described for central Alberta, notably *Corylus cornuta* Marsh., *Prunus pensylvanica* L., and *P. virginiana* var. *demissa* are either absent or very rare, while others such as *Aralia nudicaulis* and *Disporum trachycarpum* are much less common in northwestern Alberta. On the other hand, the poplar association of the latter region includes a few Cordilleran species not reported for central Alberta, e.g. *Salix scouleriana*, *Spiraea lucida*, *Arctostaphylos rubra*, *Arnica cordifolia*, and *Castilleja raupii*. Despite these and certain other differences, the poplar vegetation of central and northwestern Alberta constitutes a fairly uniform community that may well be regarded as an association, having not only the same dominant species but numerous common associates, including *Salix bebbiana*, *Rosa* spp., *Rubus pubescens*, *Fragaria glauca*, *Aster ciliolatus*, *Calamagrostis canadensis*, *Vicia americana*, *Thalictrum venulosum*, *Epilobium angustifolium*, *Galium boreale*, *Lathyrus ochroleucus*, *Pyrola asarifolia*, *Mertensia paniculata*, and *Agropyron trachycaulum*. The poplar vegetation of southwestern Alberta to which some study has been given (10) may be regarded as

a variant of the same association, including as it does a number of more southern Cordilleran elements.

Natural succession of poplar to white spruce is clearly indicated throughout the region. As has been concluded for central Alberta (9), spruce that start in a poplar stand grow slowly for many years; but, as the poplar thins out with advancing age the suppressed spruce grow rapidly and eventually come to overtop the poplar. This tendency of the spruce to supersede poplar is counteracted by biotic and pyric factors. Considerable damage is done to young spruce by snowshoe rabbits and other animals but periodic burning is the major factor operating against succession to spruce. For, while a severe burn gives only a temporary setback to the sucker-regenerating poplar, it is devastating in its effects on spruce.

As stated in an earlier paper (12), poplar and natural grassland (prairie) are close competitors in the parkland (dark soil) areas of our region. These areas are characterized by groves of trees, chiefly willow and aspen poplar and by patches of *Agropyron–Stipa–Carex* grassland (Figs. 5, 6). There is considerable evidence that these areas were originally occupied by grassland and that willows and poplars became established in small depressions and on the margins of ponds and lakes. Thence the poplars extended their roots into the surrounding grassland, producing new trees there by suckering, often bringing about the replacement of grassland by poplar vegetation. Encroachment of aspen poplar groves upon native grassland is indicated in Fig. 6, where the progressive production of aspen root suckers is to be observed in the ecotone. Counteracting this development are biotic influents, especially grazing animals and rabbits, certain edaphic factors, and periodic burning. As emphasized in the earlier paper (12), burning has doubtless been a major factor in holding back the trees and also in bringing about retrogression to grassland.

In passing, brief reference may be made to certain features of the rather unique area (Kleskun Hill), appearing in the central part of Fig. 5. This is a small "badland" area, characterized by eroded slopes, rock outcrops, sterile banks, and small salt marshes, but including also groves of white spruce, pine, and poplar, as well as patches of *Agropyron–Stipa* grassland. Creeping juniper, *Juniperus horizontalis*, is associated with spruce on a few of the more moist slopes. *Opuntia fragilis* (Nutt.) Haw. and *Lomatium villosum* Raf. occur on some of the drier, exposed situations. Occupying localized mounds on the hill is the small club moss, *Selaginella densa* Rydb., the only Peace River station for this plant known to the writer. Also, occurring in this area is the Cordilleran species, *Sedum stenopetalum* Pursh.

Concluding Remarks

Though this paper is not particularly concerned with forest site indicators, reference may be made to some earlier work designed to test Cajander's theory in Alberta. In three brief papers Brinkman considers the relative merits of liverworts (2), lichens (3), and mosses and higher plants (4), as

indicators of the quality of forest sites. Our observations lend support to Brinkman's main conclusions, especially the following. Since the continuous feather moss cover is evidently more dependent on light conditions than on moisture or soil fertility, and therefore upon the density of the stand, this cover is not characteristic of any particular site value. In an unpublished manuscript received by the writer from Brinkman, many years ago, it is stated that the true nature of the site is best indicated by the flora in open places of the stand where light has retarded the development of the mosses and allowed other species to develop, the latter being the more reliable indicators. Brinkman further suggests that the best white spruce sites are characterized by *Viburnum edule*, *Rubus idaeus*, *R. pubescens*, *Mertensia paniculata*, *Aralia nudicaulis*, and *Calamagrostis canadensis*, the poorer sites by *Elymus innovatus* and various other species. As for liverworts, we agree with Brinkman that species of *Ptilidium* occur sporadically through a wide range of site values and are probably not good site indicators. Brinkman's claim that *Jamsoniella autumnalis* and certain species of *Lophozia* show promise of being good indicators of soil and moisture conditions should be further investigated. The use of liverworts and lichens as site indicators is evidently complicated by the fact that many of these are rotten-wood and not ground species. Reference may be made here to our Notikewin stand of aspen poplar, a site of poor quality, characterized by a slow rate of tree growth and by an abundance of *Elymus innovatus* and *Shepherdia canadensis*. This stand also showed a marked decrease in rotting wood and associated lichens during a period of 20 years. A correlation between site and lichens that seemed apparent in 1931 no longer held in 1952, because of a reduction of rotting wood on the forest floor. It may be concluded, therefore, that while ground flora may often be used to advantage in interpreting site quality, due attention should be paid to developmental and historical aspects of the vegetation.

Perhaps the most controversial topic suggested by this paper is that of black spruce – white spruce relationships. In central Alberta black spruce is a tree of the muskeg. Northward it is not confined to bogs but grows also on higher ground where it is often intermixed with white spruce, birch, poplar, and pine. The tamarack too occurs outside of bogs in northern Alberta. Similar changes are known to occur with increasing altitude, as in the Caribou Mountains and in the Rocky Mountains. These changes should be studied in relation to historical events and environmental factors, such as soil temperature and length of growing season. Where black spruce grows with white spruce on higher ground, there seems to be succession to white spruce. However, this relationship should be further investigated, having in mind not only various factors that are currently effective but also such historical aspects as earlier climatic effects and priority of establishment of the two spruce species. Of interest here is the vegetation of the central part of the Mackenzie basin which Raup (16) suggests is "exceedingly young" and much of it appearing "as though it were in the process of being formed". Raup further emphasizes the difficulty of recognizing associations northward and of applying the climax

concept. While the vegetation of northwestern Alberta shows some approach to the condition described by Raup for a more northerly region, it is much more mature and relatively stable.

Attention has been drawn to the appearance of new floristic elements westward and northward in the region. This subject will receive further consideration in a forthcoming paper on bog and marsh vegetation.

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(NOTE: Tables I and VI follow.)

TABLE I

WHITE SPRUCE ASSOCIATION

(Species are arranged within subdivisions in approximate order of their abundance)

Species	Caribou Mts.	Alta.–N.W.T. Boundary	Notikewin	Saddle Hills	High Prairie	Sturgeon Lake	Lesser Slave Lake	Dawson Creek, B.C.
Trees and taller shrubs								
Picea glauca (Moench) Voss	d	d	d	d	d	d	a	d
Populus tremuloides Michx.	r,lf	o,lf	o,lf	o	s	s	f	r
Populus balsamifera L. (*P. tacamahacca* Mill.)	o,lf	o		o	r	o	s	r
Betula papyrifera Marsh	o	r	r	o	o	o	s	
Salix bebbiana Sarg.	s	o			r	s		r
Alnus rugosa (*Du Roi*) *Spreng.* var. *americana* (Regel) Fern.	o			r	o	o,la	r	
Cornus stolonifera Michx.					s	s	f	
Salix discolor Muhl.			o		r	r		
Pinus contorta Loudon var. *latifolia* Engelm.				r				s,la
Amelanchier alnifolia Nutt.						r	s	r
Abies balsamea (L.) Mill.							o,la	
Salix scouleriana Barratt							o	o
Salix myrtillifolia Anders.	o							
Salix pseudomonticola Ball	o							
Salix arbusculoides Anders.	o							
Larix laricina (Du Roi) K. Koch	o							
Sorbus scopulina Greene							r	
Lower shrubs								
Viburnum edule (Michx.) Raf.	s	s	f,la	s	f	f	a	r
Rosa acicularis Lindl. } *Rosa woodsii* Lindl. }	s	s	o	o	f	o	f	o
Lonicera involucrata (Richards.) Banks			s	o	s	s	s	r
Rubus idaeus L. vars.	o,lf		o	s.lf	r		s	
Ribes triste Pall.	o	o	s	o	o	o	s	
Ribes oxyacanthoides L.	o	r	o	o	o	o	r	
Shepherdia canadensis (L.) Nutt.	s,lf	s	r	r	s	o		o
Lonicera dioica L. var. *glaucescens* (Rydb.) Butters	r	r	r	r	r	o	r	
Vaccinium vitis-idaea L. var. *minus* Lodd.	f	a				o		f
Alnus crispa (Ait.) Pursh	s,lf		f	s			o	
Ledum groenlandicum Oeder	o,lf		r				r	f
Ribes lacustre (Pers.) Poir.	o			s			s	
Symphoricarpos albus (L.) Blake				o	r	r		
Empetrum nigrum L.	o	r						
Ribes hudsonianum Richards.	o							
Ribes glandulosum Graver				o	r			
Arctostaphylos rubra (Rehder & Wils.) Fern.	o							
Spiraea lucida Dougl.				o				r
Vaccinium caespitosum Michx.								o
Vaccinium myrtilloides Michx. (*V. canadense*)								r
Ribes ? americanum Mill.				r				

TABLE I—*Continued*

WHITE SPRUCE ASSOCIATION—*Continued*

Species	Caribou Mts.	Alta.–N.W.T. Boundary	Notikewin	Saddle Hills	High Prairie	Sturgeon Lake	Lesser Slave Lake	Dawson Creek, B.C.
Herbs								
Linnaea borealis L. var. *americana* (Forbes) Rehder	s	o	a	f,la	a	s,la	f	s,la
Cornus canadensis L.	s	f,la	f,la	f	f	f	f,la	f
Rubus pubescens Raf.	o	o	f	s	f	s	f	r
Mertensia paniculata (Ait.) G. Don	o	o	o	f	f	o	s	o
Pyrola secunda L.	o	o,lf	o	o	s	r	s	o
Pyrola asarifolia Michx.	r	o,lf	o	s	s	r	f,la	
Epilobium angustifolium L.	s	s	f	o	o	r,la	s	o
Aster conspicuus L.	s,lf		s	s	o	o,la	s	f
Equisetum arvense L.	f	s	o	f	o	s	o	
Calamagrostis canadensis (Michx.) Nutt.	o		o,la	s	f	s	f	r
Mitella nuda L.	o		s	s	f	o	f	
Fragaria glauca (S. Wats.) Rydb.	o	o		o	o	o	s	r
Galium boreale L.	o	s	o	o	f	s		o
Maianthemum canadense Desf. var. *interius* Fern.	o		s	o	f	s	o	o
Petasites palmatus (Ait.) Gray		o	o	s	f	o	s	f
Viola renifolia A. Gray	o	r	r	o	f		o	
Lathyrus ochroleucus Hook.	o	o	r	r	o	r	o	s
Aster ciliolatus Lindl. (*A. lindleyanus*)	o			r	s	o	s	o
Elymus innovatus Beal	f,la			s,la	s	s		f
Geocaulon lividum (Richards.) Fern.	s	s,lf	r,lf					o
Equisetum sylvaticum L.	s	s		s		o		
Equisetum pratense L	f, la			o		o		
Actaea rubra (Ait.) Willd. (incl. forma *neglecta* (Gillman) Robbins)	r		r	r	r	r	r	
Aralia nudicaulis L.	r		f	o	o	o	f	
Galium triflorum Michx.	r			o	o	r	o	
Lycopodium annotinum L.	o		o	r			s	r
Agropyron trachycaulum (Link) Malte				o	o	o		r
Fragaria vesca L. var. *americana* Porter			o			o	r	
Dryopteris disjuncta (Ledeb.) C. V. Mort.			r	o	r		s	
Achillea millefolium L.	o	r			r			
Disporum trachycarpum (Wats.) Benth.			r	r			o	
Delphinium glaucum Wats.	r			o		r		
Pyrola virens Schweigger	r		r		r			
Lycopodium clavatum L.						r	r	r
Goodyera repens (L.) R. Br.	r				r			r
Schizachne purpurascens (Torr.) Swallen			r			o		
Osmorhiza obtusa (Coult. & Rose) Fern.				o			r	
Arnica cordifolia Hook.				s				r
Cinna latifolia (Trev.) Griseb.				o	r			
Vicia americana Muhl.		r				o	o	
Trientalis borealis Raf.					r		r	

TABLE I—*Continued*

WHITE SPRUCE ASSOCIATION—*Continued*

Species	Caribou Mts.	Alta.–N.W.T. Boundary	Notikewin	Saddle Hills	High Prairie	Sturgeon Lake	Lesser Slave Lake	Dawson Creek, B.C.
Herbs—*Concluded*								
Hieracium umbellatum L. (*H. scabriusculum*)					r			r
Equisetum scirpoides Michx.	s							
Poa palustris L.	o							
Pedicularis labradorica Wirsing	o							
Rubus acaulis Michx.	o							
Bromus ciliatus L.					o			
Viola rugulosa Greene				o				
Carex disperma Dewey				r		r		
Dryopteris spinulosa (O. F. Muell.) Watt				r	r			
Smilacina racemosa (L.) Desf.				r			r	
Circaea alpina L.				r	r			
Smilacina stellata (L.) Desf.				r			r	
Petasites vitifolius Greene		r				r		
Lycopodium complanatum L.			r		r			
Carex deweyana Schw.				r				
Moneses uniflora (L.) A. Gray	r							
Solidago lepida DC.					r			
Thalictrum venulosum Trelease				r				
Heracleum lanatum Michx.				r				
Urtica gracilis Ait.				r				
Adoxa moschatellina L.				r				
Astragalus frigidus (L.) Gray var. *americanus* (Hook.) Wats.		r						
Parnassia palustris L. var. *neogaea* Fern.	r							
Chrysosplenium iowense Rydb.	r							
Streptopus amplexifolius (L.) DC. var. *americanus* Schultes						r		
Calypso bulbosa (L.) Oakes	r							
Corallorhiza trifida Chatelain				r				
Mosses and lichens								
Hylocomium splendens (Hedw.) Bry. Eur.	a,ld	a,ld	a,ld	a	a,ld	a	f	a,ld
Calliergonella schreberi (Bry. Eur.) Grout	s	o	s,la	f	a	a	s	a,ld
Hypnum crista-castrensis Hedw.	o		o,la	o	o	o	s	o,la
Dicranum spp. (incl. *D. bergeri* Blandow)	o	o	r	o	s	o	o	o
Aulacomnium palustre (Web. & Mohr.) Schwaegr.	s				s	s	o	s
Orthotrichum elegans Hook. & Grev.			s			s	s	
O. obtusifolium (Schrad.) Brid.								
Pylaisia polyantha Bry. Eur.		o		s		s	s	r
Polytrichum juniperinum Hedw.	o						o	o
Mnium spp. (incl. *M. cuspidatum* Hedw.)					o	s	s	
Eurhynchium strigosum (Hoffm.) Bry. Eur.		o					o	
Drepanocladus uncinatus (Hedw.) Warnst.		o					o	

TABLE I—*Concluded*

WHITE SPRUCE ASSOCIATIONS—*Concluded*

Species	Caribou Mts.	Alta.–N.W.T. Boundary	Notikewin	Saddle Hills	High Prairie	Sturgeon Lake	Lesser Slave Lake	Dawson Creek, B.C.
Mosses and lichens—*Concluded*								
Brachythecium salebrosum (Hoffm.) Br. & Sch.		o					o	
Thuidium recognitum (Hedw.) Lindb.		o					o	
Pohlia nutans (Schreb.) Lindb.							o	
Sphagnum capillaceum (Weiss) Schrank	r				r			
Rhytidiadelphus triquetrus (Hedw.) Warnst.							r	
Unspecified mosses	o	o	o	o	o	o	o	o
Peltigera aphthosa (L.) Willd.	o	o	o		o	o	s	o,la
Cladonia spp. (incl. *C. rangiferina*, *C. sylvatica*, *C. alpestris*)	s		s	o (la)		s	o	o
Usnea hirta Wigg.	s			a				a
Stereocaulon tomentosum Fr.		o	o				o	
Sticta pulmonaria (L.) Schaer.							r	
Unspecified lichens		f	o	o	o	o	o	o

TABLE II

BLACK SPRUCE ASSOCIATIONS

(Species are arranged within subdivisions in approximate order of their abundance)

Species	Feather moss				Bog moss			
	Hythe	Kinuso	Alta.–N.W.T. Boundary	Steen River	Steen River	Kenzie	Grimshaw	Ft. St. John, B.C.
Trees and taller shrubs								
Picea mariana (Mill.)BSP.	d	d	d	a,ld	a,ld	a	a	a,1d
Larix laricina (Du Roi) K. Koch	r			r	f,la		r	r
Picea glauca (Moench) Voss	s	o		s,ld				
Salix myrtillifolia Anders.	f,la	o		s	f,la	o		
Betula papyrifera Marsh		o		o		o		o
Salix bebbiana Sarg.		o	o	r		o		
Salix discolor Muhl.		o			r	o		o
Salix glauca L.			o	o	f			
Populus tremuloides Michx.			o	o,la				
Alnus rugosa (Du Roi) Spreng.				o	r			
Salix arbusculoides Anders.				r	r			
Salix scouleriana Barratt	o							
Salix ? maccalliana Rowley						r		
Salix planifolia Pursh							r	
Pinus banksiana Lamb.						r		
Pinus contorta var. *latifolia*							r	
Abies balsamea (L.) Mill.		r						

TABLE II—*Continued*

BLACK SPRUCE ASSOCIATIONS—*Continued*

Species	Feather moss				Bog moss			
	Hythe	Kinuso	Alta.–N.W.T. Boundary	Steen River	Steen River	Kenzie	Grimshaw	Ft. St. John, B.C.
Lower shrubs								
Ledum groenlandicum Oeder		f,la	f	o,la	a	a	a	a,ld
Vaccinium vitis-idaea L. var. *minus* Lodd.		f	f	s,la	a	a	f	a
Rosa acicularis Lindl. } *Rosa woodsii* Lindl. }	r	o	o	s	r			
Betula glandulosa Michx.	o				s,la		r	o,la
Vaccinium oxycoccos L.						s	f	o,la
Lonicera involucrata (Richards.) Banks	o	o						
Ribes americanum Mill.	o	s						
Ribes glandulosum Graver	o			o				
Ribes lacustre (Pers.) Poir.				o	r			
Ribes triste Pall.		o						
Ribes hudsonianum Richards.				o				
Ribes oxyacanthoides L.					r			
Shepherdia canadensis (L.) Nutt.	o			o	r			
Arctostaphylos rubra (Rehder & Wilson) Fern.				o	s,la			
Empetrum nigrum L.			s		o		r	
Myrica gale L.					o,la			
Viburnum edule (Michx.) Raf.				s				
Potentilla fruticosa L.					r			
Vaccinium myrtilloides Michx. (*V. canadense*)			r					
Herbs								
Cornus canadensis L.	o	o	o	s,la				
Petasites palmatus (Ait.) A. Gray	o	f	o	r				
Equisetum arvense L.	f,la	o	r	o	o			
Equisetum sylvaticum L.			o		s,la		r	o
Equisetum scirpoides Michx.	f,la	r	o					
Equisetum pratense L.			o	o				
Equisetum fluviatile L.								o
Carex spp.		o	o	o	o	o		o
Rubus chamaemorus L.					s	s	s	f,la
Smilacina trifolia (L.) Desf.					o	s		o
Linnaea borealis L. var. *americana* (Forbes) Rehder	f	o		s,la				
Mitella nuda L.	f	o		s				
Rubus pubescens Raf.	s	o		o				
Epilobium angustifolium L.	r		r	o	o			
Mertensia paniculata (Ait.) G. Don	r	r		s	r			
Agropyron trachycaulum (Link) Malte	o		o	s,la				
Eriophorum spissum Fern.						o	o	s
Calamagrostis sp.		o			o			r
Geocaulon lividum (Richards.) Fern.			o	r	s			
Pedicularis labradorica Wirsing			o	o				
Lathyrus ochroleucus Hook.			o	r				
Elymus innovatus Beal				f,la				
Rubus acaulis Michx.					o		r	

TABLE II—*Continued*

BLACK SPRUCE ASSOCIATIONS—*Continued*

Species	Feather moss				Bog moss			
	Hythe	Kinuso	Alta.–N.W.T. Boundary	Steen River	Steen River	Kenzie	Grimshaw	Ft. St. John, B.C.
Herbs—*Concluded*								
Galium boreale L.				o				
Pedicularis groenlandica Retz.	o							
Antennaria pulcherrima (Hook.) Greene	o							
Pyrola asarifolia Michx.				s	r			
Pyrola virens Schweigger (*P. chlorantha*)				o				
Pyrola secunda L.		r		r				
Petasites sagittatus (Pursh) A. Gray	o				r			
Petasites vitifolius Greene	o							
Fragaria sp.	o			r				
Vicia americana Muhl.	o							
Senecio pauperculus Michx.	o							
Achillea millefolium L.	r	r						
Aster ciliolatus Lindl. (*A. lindleyanus*)	r	r						
Habenaria obtusata (Pursh) Richards.				r	r			
Potentilla palustris (L.) Scop.								o
Carex capillaris L.	s						r	
Carex halleri Gunn. (*C. vahlii*)	o							
Carex saltuensis Bailey	o							
Carex aurea Nutt.	o							
Carex canescens L.								o
Aralia nudicaulis L.		r						
Maianthemum canadense Desf. var. *interius* Fern.				r				
Lycopodium annotinum L.				r				
Corallorhiza trifida Chatelain				r				
Astragalus frigidus (L.) Gray var. *americanus* (Hook.) S. Wats.				r				
Viola renifolia A. Gray				r				
Solidago lepida DC.	r							
Bryophytes and lichens								
Hylocomium splendens (Hedw.) Bry. Eur.	f,la	f,ld	a,ld	a,ld	f			r,la
Aulacomnium palustre (Web. & Mohr.) Schwaegr.	a,ld	o	o,la	o	f	f		
Sphagnum capillaceum (Weiss) Schrank		s,ld		r	o	f		f,la
Calliergonella schreberi (Bry. Eur.) Grout		f,ld	s	s,la				o
Sphagnum fuscum (Schimp.) H. Klinggr.		r				a	a	a
Polytrichum juniperinum Willd.		o		o		o	o	o
Hypnum crista-castrensis Hedw.		f,ld		r				
Camptothecium nitens (Schreb.) Schimp.	a,ld				o		r	
Ptilidium sp.			s	o				
Sphagnum tenerum Sull. & Lesq.						o		r
Sphagnum girgensohnii Russow						o		
Sphagnum recurvum Beauv.						o	o	
Dicranum bergeri Blandow	r	r						

TABLE II—*Concluded*

BLACK SPRUCE ASSOCIATIONS—*Concluded*

Species	Feather moss				Bog moss			
	Hythe	Kinuso	Alta.–N.W.T. Boundary	Steen River	Steen River	Kenzie	Grimshaw	Ft. St. John, B.C.
Bryophytes and lichens—*Concluded*								
Dicranum bonjeani DeNot			r				r	
Mylea anomala (Hook.) S. F. Gray								o
Tetraplodon angustatus (Sw.) B. & S.								r
Pohlia nutans (Schreb.) Lindb.				r				
Unspecified mosses	r	r	o	o	s	o		o
Peltigera aphthosa (L.) Willd.	s,la	o	s	s	o			o
Usnea hirta Wigg.	f	a						f
Parmelia saxatilis Ach.	f							
Cladonia sylvatica (L.) Hoffm.			s	f				
Cladonia rangiferina (L.) Web.			f					
Cladonia alpestris (L.) Rabenh.				o				
Cladonia spp.	o	o		r	f	f	a	a
Cetraria nivalis Ach.				r				
Icmadophila aeruginota (Scop.) Trevis						o	r	
Unspecified lichens	s	f	o	o	o	o	r	o

TABLE III

QUADRAT RECORDS (PERCENTAGE GROUND COVER) FOR A VARIANT OF THE BLACK SPRUCE – FEATHER MOSS ASSOCIATION

Species	Quadrats									
	1	2	3	4	5	6	7	8	9	10
Hylocomium splendens	80	55	25	5	30	30	75	80	80	80
Calliergonella schreberi	6			5						1
Dicranum sp.									1	
Other mosses			2	1	2					
Ptilidium sp.							1			
Peltigera aphthosa						20				
Cladonia sp.									2	
Various lichens		3		1	2		2			2
Bare ground		30	6	60	5	2				
Linnaea borealis	4	2	25	2	2	15	2	3	4	
Cornus canadensis	4	6	2	1	20	2		15		8
Grasses, chiefly *Agropyron trachycaulum*	2	1	20	15	25	5	1			1
Rosa acicularis	2	1	8	3	2	10			2	1
Pyrola asarifolia		1	3	1	2	15			2	
P. secunda		1			2				2	
Vaccinium vitis-idaea							18		4	
Rubus pubescens			3	3	2					
Mertensia paniculata			2	3	4			1		1
Equisetum scirpoides									1	5
E. pratense							1		2	
Viburnum edule			4		2					
Shepherdia canadensis	1					1				
Ribes sp.								1		1
Fragaria sp.	1									

TABLE IV

PINE VEGETATION

(Species are arranged within subdivisions in approximate order of their abundance)

Species	Smith	Peace River	Grande Prairie	Saddle Hills	Hawk Hills	Taylor, B.C.	Ft. St. John, B.C.
Trees and taller shrubs							
Pinus contorta Loudon var. *latifolia* Engelm.		r	a	a	d	d	d
Pinus banksiana Lamb.	d	d	f				
Picea glauca (Moench) Voss	r	r	r	s	o,la	o	o
Populus tremuloides Michx.	o	r	o	o	o	o	s
Betula papyrifera Marsh	o	o		r	r		r
Salix bebbiana Sarg.	o	o	o	r	o	o	
Salix scouleriana Barratt		r	r	s	s	s	r
Amelanchier alnifolia Nutt.	o	s	o	o			
Populus balsamifera L. (*P. tacamahacca* Mill.)			r	o		o	
Salix discolor Muhl.	r		r			s	
Prunus virginiana L. var. *demissa* (Nutt.) Torr.	r		s				
Prunus pensylvanica L.	r			o			
Lower shrubs							
Rosa acicularis Lindl.	s	s	s	f	o	f	o
Rosa woodsii Lindl.							
Alnus crispa (Ait.) Pursh	s		s	s,la	f,la		f
Arctostaphylos uva-ursi (L.) Spreng.	o,la	a	f,la	f,la	r		
Vaccinium vitis-idaea L. var. *minus* Lodd.	s,la	s,la	s,la		f		
Shepherdia canadensis (L.) Nutt.		o	o	s	s		
Vaccinium myrtilloides Michx. (*V. canadense*)	s		s		o,la		
Spiraea lucida Dougl.			r	s		o	o
Viburnum edule (Michx.) Raf.				s,la	r	f,la	
Rubus idaeus L. vars.	o			o		r	o
Vaccinium caespitosum Michx.				o	s	o	
Lonicera dioica L. var. *glaucescens* (Rydb.) Butters		r		o		r	
Ledum groenlandicum Oeder	r				s		
Lonicera involucrata (Richards.) Banks				o			r
Juniperus horisontalis Moench		r	r				
Elaeagnus commutata Bernh.		o					
Ribes triste Pall.							o
Ribes oxyacanthoides L.							o
Ribes sp.						r	
Cornus stolonifera Michx.		r					
Betula glandulosa Michx.					r		
Juniperus communis L. var. *saxatilis* Pallas		r					
Symphoricarpos albus (L.) Blake				s			
Herbs							
Linnaea borealis L. var. *americana* (Forbes) Rehder	s,la	o,la	a	f,la	f	a	a
Cornus canadensis L.	s	f	s	f	f	f	f
Elymus innovatus Beal	f,la	f,la	s	s	f,la	o	
Maianthemum canadense Desf. var. *interius* Fern.	s,la	s	o	s		o	f
Pyrola secunda L.	o,la		o	o	s	o	s,la
Lathyrus ochroleucus Hook.	o	s	o	f	r	r	o
Epilobium angustifolium L.	r	o	r	o	o	r	o
Fragaria glauca (S. Wats.) Rydb.	o	r	s	s		o	o

TABLE IV—*Continued*

PINE VEGETATION—*Continued*

Species	Smith	Peace River	Grande Prairie	Saddle Hills	Hawk Hills	Taylor, B.C.	Ft. St. John, B.C.
Herbs—*Continued*							
Galium boreale L.	o	s	s			r	o
Rubus pubescens Raf.	o			o	o	o	s
Carex siccata Dewey	s,la		f	o		r	
Calamagrostis spp.		r	r	s		s,la	s
Artemisia caudata Michx. (incl. var. *calvens* Lunell)	s	o	f			r	
Hieracium umbellatum L. (*H. scabriusculum* Rydb.)	o	o	s	o			
Solidago missouriensis Nutt.	o	o	s		o		
Solidago decumbens Greene var. *oreophila* (Rydb.) Fern.	o	o	s				
Orysopsis pungens (Torr.) Hitchc.	s,la	s,la	s,la				
Festuca saximontana Rydb.	s,la	o	s,la				
Lilium philadelphicum L. var. *andinum* (Nutt.) Ker	o	s	o	o			
Pulsatilla ludoviciana (Nutt.) Heller	s	o	s				
Anemone multifida Poir. var. *hudsoniana* DC.	s	o	s				
Petasites palmatus (Ait.) A. Gray				o	r	r	o
Pyrola virens Schweigger (*P. chlorantha*)	o			r		r	o
Aralia nudicaulis L.	o			s			f
Aster ciliolatus Lindl. (*A. lindleyanus*)	o			o		f,la	
Pyrola asarifolia Michx.				o	s		o
Equisetum sylvaticum L.	o			s		o	
Aster conspicuus L.				f			s,la
Erigeron glabellus Nutt.	s		s				
Campanula rotundifolia L.	o	r	o				
Arnica cordifolia Hook.				s		o	o
Vicia americana Muhl.		s				o	o
Schizachne purpurascens (Torr.) Swallen					s		r,la
Equisetum hyemale L. var. *affine* (Engelm.) A.A.Eat.	o		o				
Comandra pallida A.DC.		o	o				
Androsace septentrionalis L.	o,la		o				
Viola renifolia A. Gray					r	r	s,la
Mertensia paniculata (Ait.) G. Don				o			o
Aster laevis L.	o		o				
Astragalus striatus Nutt.	o		o				
Lycopodium annotinum L.				r			f,la
Agropyron trachycaulum (Link) Malte, incl. *A. pauciflorum* (Schw.) Hitchc. and *A. subsecundum* (Link) Hitchc.			o	o			
Arabis holboellii Hornem. var. *retrofracta* (Grah.) Rollins		r	o				
Viola adunca J. E. Smith	o	r					
Equisetum arvense L.	o					r	
Smilacina stellata (L.)Desf.	r		o				
Bromus pumpellianus Scribn.		r	o				
Achillea millefolium L.	r		r				
Astragalus aboriginorum Richards.	r		r				
Apocynum androsaemifolium L.		r	r				
Arceuthobium americanum Nutt.			f				
Galium triflorum Michx.							o
Thalictrum sp.							o
Carex umbellata Schkuhr	o						
Osmorhiza sp.							o
Viola rugulosa Greene							o

TABLE IV—*Concluded*

PINE VEGETATION—*Concluded*

Species	Smith	Peace River	Grande Prairie	Saddle Hills	Hawk Hills	Taylor, B.C.	Ft. St. John, B.C.
Herbs—*Concluded*							
Equisetum pratense L.	o						
Arabis lyrata L. var. *kamchatica* Fischer	o						
Stellaria sp.	r						
Aquilegia brevistyla Hook.			r				
Senecio pauperculus Michx.			r				
Castilleja raupii Pennell					r		
Geocaulon lividum (Richards.) Fern.					r		
Disporum trachycarpum S. Wats.				r			
Pedicularis labradorica Wirsing					r		
Carex richardsonii R. Br.			r				
Agrostis scabra Willd.						r	
Gentiana amarella L.						r	
Astragalus alpinus L.					r		
Melampyrum lineare Lam.		r					
Bryophytes and lichens							
Hylocomium splendens (Hedw.) Bry. Eur.	o,la	f,la	o	f,la	f	f,la	a
Calliergonella schreberi (Bry. Eur.) Grout	o,la	s,la	r	o,la	o	o,la	a
Polytrichum piliferum Schreb.	f,la	s	f,la		s	o	
Polytrichum juniperinum Willd.	s,la			s	f	s,la	o
Dicranum spp. incl. *D. bergeri* Blandow and *D. rugosum* (Hoff.) Brid.	r	o	r	o		r	o
Ceratodon purpureus Brid.	s	o	s			o	
Hypnum crista-castrensis Hedw.	r			r,la		o	o
Drepanocladus sp.					s		
Other mosses	o	r	s	o	o	o	
Ptilidium ciliare (L.) Nees.						r	
Ptilidium pulcherrinum (Web.) Hampe						o	
Cladonia mitis Sandst.	f,la	f,la	f,la				
Cladonia gracilis (L.) Willd. var. *dilatata* (Hoffm.) Vainio	f,la				f,la		
Cladonia multiformis Merrill f. *subascypha* (Vainio) Evans	o				f		
f. *simulata* Robbins	o						
Cladonia cornutoradiata (Coera) Sandst. f. *repititoprolifera* Sandst.					o		
f. *radiata* (Schreb.) Sandst.	o						
Cladonia coccifera (L.) Willd.	o				o		
Cladonia verticellata (Hoffm.) Schaer. f. *involuta* (Th.Fr.) Stein.	s						
Cladonia cornuta (L.) Hoffm. f. *cylindrica* Schaer.					s		
Cladonia deformis (L.) Hoffm.					o		
Cladonia turgida (Ehrh.) Hoffm.	o						
Cladonia spp.		s	s	f		f	o
Peltigera aphthosa (L.) Willd.	s				o		
Peltigera canina (L.) Willd. incl. f. *membranacea* (Ach.) Duby	s		s		f		
Peltigera spp.		o		o		f	o
Cetraria islandica (L.) Ach.			s,la				
Cetraria cucullata (Bellard) Ach.			r				
Cetraria pinastri (Scop.) Röhl.	r						
Stereocaulon tomentosum Fries					o		
Evernia prunastri (L.) Ach.			o				

TABLE V

BALSAM POPLAR CONSOCIATION

(Species are arranged within subdivisions in approximate order of their abundance)

Species	High Prairie	Smoky River	Wanham	Sturgeon Lake	Rolla, B.C.	Dawson Creek, B.C.
Trees and taller shrubs						
Populus balsamifera L. (*P. tacamahacca* Mill.)	d	a,ld	a,ld	d	a,ld	a,ld
Populus tremuloides Michx.	s	o	f	o,la	f	s
Cornus stolonifera Michx.	f	f	f	o	f	o,la
Salix bebbiana Sarg.	s	r	s	s	o	o,la
Alnus rugosa (Du Roi) Spreng. var. *americana* (Regel) Fern.		f		s,la	f	s,la
Picea glauca (Moench) Voss		r			f	r
Betula papyrifera Marsh		r		r	r	o
Pinus contorta Loudon var. *latifolia* Engelm.					r	o,la
Salix scouleriana Barratt					o	o
Salix discolor Muhl.	o			o		o
Salix pseudomonticola Ball	r					
Salix lasiandra Benth.		r				
Viburnum trilobum Marsh (*V. opulus* var. *americanum*)		r				
Elaeagnus commutata Bernh.		r				
Amelanchier alnifolia Nutt.				r		
Lower shrubs						
Rosa acicularis Lindl. } *Rosa woodsii* Lindl. }	o	o	s	f	s	f
Rubus idaeus L. vars.	s	r	r	s	o	o
Lonicera involucrata (Richards.) Banks	s	r	r	f	o	o
Ribes oxyacanthoides L.	o	r		o	o	r
Viburnum edule (Michx.) Raf.		r		f	o	o
Symphoricarpos albus (L.) Blake		r	o	o		r
Alnus crispa (Ait.) Pursh					o	s,la
Shepherdia canadensis (L.) Nutt.		r			r	r
Spiraea lucida Dougl.					o	r
Ribes triste Pall.	s					
Ribes hirtellum Michx.	o					
Ribes americanum Mill.		r				
Herbs						
Calamagrostis canadensis (Michx.) Nutt.	f	s	s	f	s	a
Rubus pubescens Raf.	o	o	s	f	f	f,la
Equisetum arvense L.	s	o	s	s	o	o
Aster ciliolatus Lindl. (*A. lindleyanus*)	o	r	s	s	f	f
Fragaria glauca (S. Wats.) Rydb.	s	r	s	s	o	s
Epilobium angustifolium L.		o	s	o	o	o,la
Mertensia paniculata (Ait.) G. Don	o		r	f	f,la	f
Thalictrum venulosum Trelease	s	o	o			r
Vicia americana Muhl.	o	r	s	r	o	
Galium boreale L.		r	o	s	o	o
Pyrola asarifolia Michx.		f		s	f	o,la
Lathyrus ochroleucus Hook.		r		s	f	f
Agropyron trachycaulum (Link.) Malte (vars.)		r	s	o	f	
Equisetum pratense L.	o	o	s			
Aster conspicuus Lindl.			r	o	s	f
Galium triflorum Michx.	s	r	o	s		

TABLE V—*Continued*

BALSAM POPLAR CONSOCIATION—*Continued*

Species	High Prairie	Smoky River	Wanham	Sturgeon Lake	Rolla, B.C.	Dawson Creek, B.C.
Herbs—*Concluded*						
Bromus ciliatus L.	o		o	r		o
Petasites sagittatus (Pursh) A. Gray	o		o		r	
Solidago gigantea Ait. var. *leiophylla* Fern.	r	s	o			
Linnaea borealis (L.) var. *americana* (Forbes) Rehder				s,la	o,la	o,la
Smilacina stellata (L.) Desf.	o	s	o			
Petasites palmatus (Ait.) A. Gray				s	f	s
Anemone canadensis L.	o		s			
Stachys palustris L. var. *pilosa* (Nutt.) Fern.	r	r	o			
Achillea millefolium L.	r	r		r		r
Actaea rubra (Ait.) Willd., incl. forma *neglecta* (Gillman) Robbins	r	r		o		r
Mitella nuda L.	o			s	o	
Aster coerulescens DC.		o	r			
Pyrola secunda L.				o	o	r
Fragaria vesca L. var. *americana* Porter		r		s	r	r
Poa palustris L.		r	s	o		
Cornus canadensis L.			r	s		o
Aralia nudicaulis L.		r		o		r
Viola renifolia A. Gray			o	o		
Equisetum sylvaticum L.				s		
Carex bebbii Olney			o			
Geum macrophyllum Willd.	o					
Viola rugulosa Greene		r		r		r
Achillea sibirica Ledeb. (*A. multiflora*)			o			
Solidago lepida DC.	r		r	r		
Heracleum lanatum Michx.	r			o		
Maianthemum canadense Desf. var. *interius* Fern.		r		s		
Arnica cordifolia Hook.					r	
Aster sibiricus L. var. *meritus* (A. Nels.) Raup		r				
Potentilla norvegica L.			r			
Senecio eremophilus Richards.			r			
Mentha arvensis L. var. *glabrata* (Benth.) Fern.			r			
Hieracium umbellatum L. (*H. scabriusculum*)			r			
Osmorhiza obtusa (C. & R.) Fern.				s		r
Smilacina racemosa (L.) Desf.						r
Ranunculus macounii Britt.			r			
Elymus canadensis L.		r				
Astragalus canadensis L.		r				
Astragalus tenellus Pursh		r				
Arenaria laterifolia L.						r
Schizachne purpurascens (Torr.) Swallen				r		
Carex deweyana Schwein.				r		
Dryopteris spinulosa (O. F. Muell.) Watt				r		

TABLE V—*Concluded*

BALSAM POPLAR CONSOCIATION—*Concluded*

Species	High Prairie	Smoky River	Wanham	Sturgeon Lake	Rolla, B.C.	Dawson Creek, B.C.
Bryophytes and lichens						
Pylaisia polyantha Bry. Eur.	o	o		f	f	f
Mnium spp. (incl. *M.cuspidatum* Hedw.)	s	o			o	
Brachythecium spp.	o	o	s			
Orthotrichum spp.	o	o				
Hylocomium splendens (Hedw.) Bry. Eur.				o	o	r,la
Calliergonella schreberi (Bry. Eur.) Grout				o	o	
Drepanocladus uncinatus (Hedw.) Warnst.					o	
Aulacomnium palustre (Web. & Mohr.) Schwaegr.					o	
Polytrichum juniperinum Willd.					o	
Eurynchium strigosum (Hoffm.) Bry. Eur.				o		
Dicranum spp.				o	o	
Hypnum crista-castrensis Hedw.					r	
Unspecified mosses	s	s	s	s	o	o,la
Cladonia spp.					o	o
Peltigera spp.				o	o	r
Unspecified lichens	o	o	o	r	o	o

TABLE VI

ASPEN POPLAR CONSOCIATION

(Species are arranged within subdivisions in approximate order of their abundance)

Species	Steen River	Fort Vermilion	Keg River	Notikewin	Nampa	High Prairie	Saddle Hills	Hythe	Alta.–B.C. boundary	Fort St. John, B.C.
Trees and taller shrubs										
Populus tremuloides	d	d	d	d	d	d	d	d	d	d
Populus balsamifera (*P. tacamahacca*)		o	s	o	r	o	s		o	o,la
Salix bebbiana	s	s	s	s	s	s	o	s	o	o
Salix discolor		o	o	o	f	o			o	
Picea glauca	o	o		r	r	r	r			r
Amelanchier alnifolia	o	s			s			r	r	r
Cornus stolonifera	r		o	r	r	s		r		
Salix scouleriana				o			s		o	f
Betula papyrifera				r		r	o		o	
Pinus banksiana	o				r					
Pinus contorta var. *latifolia*							r		r	
Prunus virginiana var. *demissa*									r	
Salix pseudomonticola			r							
Salix arbusculoides			r							
Salix gracilis (*S. petiolaris*)		r								
Larix laricina	r									
Alnus rugosa var. *americana*							r			

TABLE VI—*Continued*

ASPEN POPLAR CONSOCIATION—*Continued*

Species	Steen River	Fort Vermilion	Keg River	Notikewin	Nampa	High Prairie	Saddle Hills	Hythe	Alta.–B.C. boundary	Fort St. John, B.C.
Lower shrubs										
Rosa acicularis }	s	a	f	s	a	f	f	f	f	f
Rosa woodsii }										
Viburnum edule	s		o	s,la	o	s	f,la	o,la	f,la	a
Symphoricarpos albus		o		o	o	s	o	f		o
Shepherdia canadensis	a			f,la	s	o			o	s
Rubus idaeus vars.		o	s		o		o	f		o
Lonicera dioica var. *glaucescens*	o			r	o	r	o	s		
Ribes oxyacanthoides	r		s		r	o	o	o		
Arctostaphylos uva-ursi	a			r,la		r	r		o	
Lonicera involucrata					r	o	r	s	r	o
Spiraea lucida							s,la		o	f
Alnus crispa			o				f			a
Ledum groenlandicum	o			r					r	
Vaccinium vitis-idaea var. *minus*	f,la								s	
Vaccinium caespitosum				r					s	
Ribes glandulosum								r		r
Ribes hirtellum						o				
Ribes triste						o				
Arctostaphylos rubra	o									
Ribes hudsonianum						r				
Vaccinium myrtilloides (*V. canadense*)									r	
Clematis verticellaris var. *columbiana*							r			
Herbs										
Vicia americana	o	s	o	s	f	o	o	o	f	s
Lathyrus ochroleucus	s	o	s	f	o	o	o	o	f	o
Fragaria glauca	o	f	a	o	f	s	s	o	o	o
Galium boreale	s	o	s	o	f	s	o	f	o	s
Epilobium angustifolium	s	s	s	s	f	o	f	o	f	o
Cornus canadensis	f,la		o	f	f	s	f	f,la	f,la	s
Rubus pubescens		s	f,la	s	f	s	s	s	s	f
Calamagrostis canadensis		s	f	s,la	a		f	f	f	s
Agropyron trachycaulum (incl. *A. pauciflorum* and *A. subsecundum*)		s	o	o	f	s	o	f		o
Pyrola asarifolia	s		s	s,la	o	o	s,la		f,la	s
Maianthemum canadense var. *interius*	o	s		f	s	r	s		s	o
Elymus innovatus	f,la	o		f.la	f		f.la		f.la	f
Aster ciliolatus (*A. lindleyanus*)		s		s	f	s	f	o	f	o
Linnaea borealis var. *americana*				f,la	o.la	s	s,la		a	s,la
Mertensia paniculata			f	o	f	s	o	s	o	s
Petasites palmatus			o	s	o	o	s		s	o
Pyrola secunda	o	o		s	r		s		s	o
Equisetum arvense		o	a	o	o				o	o
Thalictrum venulosum			o		o,la		o	s		o
Aster conspicuus				s	r		f,la		s	f,la
Bromus ciliatus		o		r	s	r	o	r		
Aralia nudicaulis				r,la		s	s			f
Viola renifolia			o		r	r	o		o	o
Schizachne purpurascens		f		o		r		s		
Poa palustris		s			r	o		s		
Arnica cordifolia							s,lf	o	o	o
Viola rugulosa						s		r		o

TABLE VI—*Continued*

ASPEN POPLAR CONSOCIATION—*Continued*

Species	Steen River	Fort Vermilion	Keg River	Notikewin	Nampa	High Prairie	Saddle Hills	Hythe	Alta.–B.C. boundary	Fort St. John, B.C.
Herbs—*Concluded*										
Hieracium umbellatum (*H. scabriusculum*)		o			r	o	r			
Fragaria vesca var. *americana*			o	r	o		r			
Actaea rubra (incl. forma *neglecta*)					r	r	r	s		r
Achillea millefolium		r		r	o				r	
Equisetum sylvaticum				s	o		o			
Mitella nuda						r	o			o
Galium triflorum					r		o	r		r
Castilleja ? miniata (*C. rhexifolia*)					o	r			r	r
Solidago lepida					f			r		r
Senecio pauperculus				r	r	r			r	
Gentiana amarella		o			r	r				
Petasites vitifolius			o	r	r					
Smilacina stellata		o						o		
Equisetum pratense		o					o			
Solidago gigantea var. *leiophylla*					f	r				
Arenaria lateriflora		r			r			o		
Heracleum lanatum					r		o	r		
Campanula rotundifolia		r			r			r		
Disporum trachycarpum						o				r
Geum ? macrophyllum		r			r			r		
Osmorhiza obtusa						r	r			r
Delphinium glaucum		r						r		
Petasites sagittatus			r		r					
Trientalis europaea var. *arctica*				r		r				
Achillea sibirica (*A. multiflora*)					r	r				
Potentilla norvegica		r				r				
Viola adunca		r			r					
Lycopodium complanatum	f									
Halenia deflexa					r	r				
Thalictrum occidentale var. *palouense*		o								
Pyrola elliptica		o								
Bromus pumpellianus		o								
Corallorhiza trifida			r							
Castilleja raupii				r						
Castilleja ? rhexifolia							r			
Stachys palustris var. *pilosa*					r					
Arnica chamissonis					r					
Geranium bicknellii					r					
Pyrola virens (*P. chlorantha*)	r									
Comandra pallida		r								
Smilacina amplexicaulis						r				
Moneses uniflora							r			
Stellaria crassifolia						r				
Stellaria longipes						r				
Stellaria longifolia								r		
Dryopteris spinulosa								r		
Carex aenea									r	
Carex aurea					r					
Carex praticola					r					
Agrostis scabra					r					
Bryophytes and lichens										
Pylaisia polyantha	f	f	s	a	a	s	s	f	f	f
Hylocomium splendens	o		o	s,la	o	a	o	s	o	s
Aulacomnium palustre			r		o	o	o	o	s	s

TABLE VI—*Concluded*

ASPEN POPLAR CONSOCIATION—*Concluded*

Species	Steen River	Fort Vermilion	Keg River	Notikewin	Nampa	High Prairie	Saddle Hills	Hythe	Alta.–B.C. boundary	Fort St. John, B.C.
Bryophytes and lichens—*Concluded*										
Calliergonella schreberi				o	r		o	o	o	o
Drepanocladus uncinatus			s	s	o				o	
Polytrichum juniperinum	o	r		o		r			o	
Mnium spp.					o	o		o		o
Dicranum spp. (incl. *D. bergeri*)	o		o						o	o
Pohlia nutans				o				o	o	
Hypnum crista-castrensis								o		o
Brachythecium oxycladon									o	
Ceratodon purpureus				s					o	
Climacium americanum						o				
Tetraplodon angustatus								r		
Unspecified mosses		s		o	o		o			o
Ptilidium pulcherrimum				o				o	o	
Ptilidium ciliare								o	o	
Peltigera aphthosa	o	o		f	o	o	o	o,la	o	o
Cladonia spp.	o					o	o	f	o	o
Cladonia rangiferina			f							
Cladonia turgida			o							
Cladonia gracilis			o			o				
Cladonia fimbriata			o							
Cladonia sylvatica						o				
Parmelia physodes								o		
Stereocaulon tomentosum				o						
Unspecified lichens					o		o			

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Contents

PAGE

Nutritional Requirements of *Arthrobacter terregens*—*Margaret O. Burton and A. G. Lochhead* - - - - - - - - - - - - 145

Fertility and Polyploidy of *Euphorbia cyparissias* in Canada—*R. J. Moore and D. R. Lindsay* - - - - - - - - - - - - 152

Phylogeny of *Carex* in the Light of Parasitism by the Smut Fungi—*D. B. O. Savile and J. A. Calder* - - - - - - - - - - - 164

Studies in Forest Pathology. X. Decay of White Pine in the Timagami Lake and Ottawa Valley Areas—*L. T. White* - - - - - - - - 175

Isolation of Bacteriophages for the Detection and Identification of Some Seed-borne Pathogenic Bacteria—*M. D. Sutton and H. Katznelson* - - - 201

Nitrogen and Vitamin Requirements of *Pseudomonas hydrophila*—*Florence R. Tamboline* - - - - - - - - - - - - - 206

Forest Communities in Northwestern Alberta—*E. H. Moss* - - - - 212